IMPORTANCE OF HETEROGENEITY IN A GRASSLAND ECOSYSTEM

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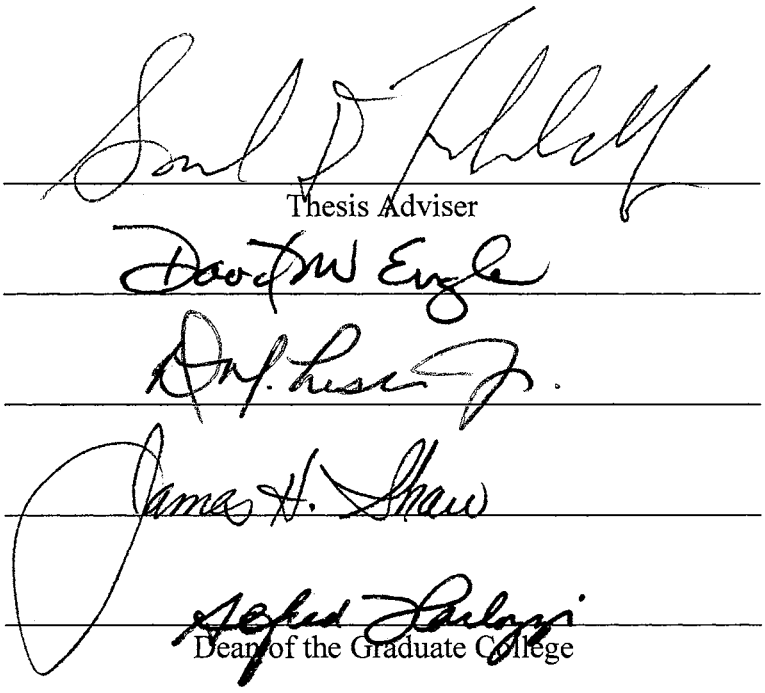

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INTRODUCTION

This dissertation is composed of 3 manuscripts formatted for submission to scientific journals: *Ecological Applications* (Chapter II), *Conservation Biology* (Chapter III), and *Journal of Applied Ecology* (Chapter IV).

CHAPTER 2

INFLUENCE OF MANAGEMENT-IMPOSED HETEROGENEITY ON A GRASSLAND AVIFAUNAL COMMUNITY

ABSTRACT

Disturbance-driven spatial heterogeneity is critical for maintaining many declining species in grasslands. In tallgrass prairie, disturbances such as grazing and fire generate patchiness across the landscape contributing to a "shifting mosaic" that presumably enhances biodiversity. Grassland birds have species-specific vegetation structural requirements, and bird community dynamics can be monitored to assess the ecological influence of disturbance-induced spatial heterogeneity. We experimentally altered spatial heterogeneity of vegetation structure within a tallgrass prairie by varying the spatial and temporal extent of fire and by introducing herbivores (patch treatment). We contrasted this disturbance regime with a relatively uniform application of fire and grazing (traditional treatment). We monitored grassland bird abundance during the breeding season in 2001 to 2003 to determine the influence of altered spatial heterogeneity on the grassland bird community. Patch burning and interactive effects of grazing resulted in a more spatially heterogeneous landscape than a uniform application of fire and grazing. This led to greater variability in the grassland bird community with one species, Henslow's sparrow (*Ammodramus henslowii*), only occurring within the patch treatment. Bird abundance within species varied among patch types and treatments

in accordance with structural requirements of species reported in past literature. Our study demonstrates that increasing the spatial and temporal heterogeneity of disturbance may favor several declining grassland bird species. However, the role of spatial heterogeneity and variable disturbance regimes in maintaining or enhancing biological diversity in general should be more thoroughly scrutinized to further explore the mechanisms involved.

Keywords: disturbance, diversity, fire, grassland birds, grazing, heterogeneity, rangelands, shifting mosaic, tallgrass prairie

INTRODUCTION

Heterogeneity is critical for the maintenance of many ecosystems and is considered important in the design of conservation strategies (Christensen 1997, Ostfeld et al. 1997, Wiens 1997, Fuhlendorf and Engle 2004). In fact, some have suggested that spatial heterogeneity interacting with other landscape features maintains biological diversity and should be a foundation of ecosystem management (Christensen 1997, Ostfeld et al. 1997, Fuhlendorf and Engle 2001). Habitat heterogeneity is positively correlated with diversity of several faunal groups including birds, amphibians, reptiles, and lepidopterans (Atauri and de Lucio 2001, Tews et al. 2004). Variable disturbance regimes overlaid on existing heterogeneous geomorphological features often create patchiness across the landscape, contributing to a shifting mosaic, potentially enhancing biodiversity (Burnett et al. 1998). Most models for managing ecosystems do not consider the influence of disturbance regimes on spatial or temporal variability (Fuhlendorf and Engle 2001). To describe and manage disturbance processes in ecosystems, it is essential

that we understand spatial and temporal variability that is driven by disturbance processes.

The interaction of grazing and fire within an already heterogeneous tallgrass-prairie landscape can increase patchiness at multiple scales and may play a role in maintaining biodiversity (Vinton et al. 1993, Hartnett et al. 1996). The fire-grazing model predicts that bison (*Bos bison*) preferentially select high-quality vegetation regrowth within recently burned parts of the landscape (Coppedge and Shaw 1998). When only one part of the landscape available to herbivores is burned, intense grazing occurs on burned patches while adjacent, unburned patches remain relatively ungrazed. Abundant fuel in unburned patches leads to a higher probability of future fires within these patches, while fuel reduction in burned and focally grazed patches leads to a lower probability of reoccurring fire, allowing fuel accumulation. Thus, fire alters grazing decisions of herbivores, and grazing influences the extent and intensity of future fires. This grazing-fire interaction (grazing-fire model) results in a shifting mosaic of plant communities across the landscape, with some patches containing a grazing lawn that was recently burned and grazed and other patches consisting of tall, comparatively undisturbed vegetation (Steuter 1986, Hobbs et al. 1991, Hamilton 1996). Grassland-obligate wildlife species evolved within the context of this shifting mosaic, with some species adapted to a fairly narrow range of patch types created under spatially and temporally distinct disturbance regimes.

Many bird species are sensitive to structural changes in grasslands on vegetation so birds are excellent indicator species of change in ecosystem structure and function (Knopf 1994, Askins 2000). Structural heterogeneity of vegetation strongly influences

grassland bird communities (MacArthur and MacArthur 1961, Wiens 1974, Walk and Warner 2000), with some bird species preferring grassland habitats with certain patch structural characteristics (Cody 1985). For example, abundance of dickcissels (*Spiza americana*) is correlated positively with vertical cover and percent forb cover, whereas abundance of grasshopper sparrow (*Ammondramus savannarum*) in tallgrass prairie is correlated negatively with vertical cover (Zimmerman 1982, Hughes et al. 1999). Upland sandpipers (*Bartramia longicauda*) and lark sparrows (*Chondestes grammacus*) prefer highly disturbed areas containing short vegetation and bare ground (Bock et al. 1984), whereas Henslow's sparrows require undisturbed grasslands with accumulated litter and dead grass cover (Cully and Michaels 2000). Variability in habitat selection of these species suggests that heterogeneous grasslands maintained by spatially and temporally variable disturbances are required to maintain species richness within this imperiled bird guild (Askins 2000).

Current management of grasslands for agricultural production typically reduces inherent spatial and temporal habitat heterogeneity within landscapes through uniform application of fire and grazing (Holechek et al. 2003). This management model assumes that decreased spatial heterogeneity increases livestock production and reduces ecosystem degradation; however, this conjecture has been based on spatially fixed herbivore activity (Fuls 1992, Bailey et al. 1998, Holechek et al. 2003). Grassland-dependent birds may be declining in part due to management driven reductions in heterogeneity on grasslands by promoting uniform and moderate disturbance that minimizes heavily disturbed and undisturbed plant communities (Knopf 1994). We wanted to test the utility of the grazing-fire model in the context of conservation of

grassland bird diversity. Therefore, we compared the traditional, homogeneous management model to the grazing-fire model in which heterogeneity is based on evolutionary grazing and fire interactions (Fuhlendorf and Engle 2001). To our knowledge, a management model that uses a shifting mosaic to increase heterogeneity has not been compared to a traditional, homogenous management model within a replicated experiment.

Therefore, our objectives were to test 1) if altering the temporal and spatial pattern of fire and grazing in a tallgrass prairie would result in a shifting mosaic of vegetation composition and structure compared with traditional management in which fire and grazing are applied annually in a spatially uniform pattern and 2) if a shifting mosaic would result in increased heterogeneity at a higher trophic level, specifically in the grassland bird community, than traditional management. We predicted that application of spatially variable fire and grazing in tallgrass prairie would increase spatial heterogeneity, thus allowing coexistence of a suite of grassland bird species with more breadth in habitat structure requirements.

METHODS

Site description

Our study took place on the Tallgrass Prairie Preserve (TGPP) in northcentral Oklahoma, USA (36° 50′N, 96° 25′W), owned and operated by The Nature Conservancy. The Preserve lies within the southern portion of the Flint Hills region of the Great Plains and contains one of the last remaining examples of large, uncultivated tallgrass prairie habitats in North America. The climate is temperate, with hot summers

(average high of 33.9 C for July 2001 to 2003) and cold winters (average low of -4.8 C for January 2001 to 2003). Growing-season (April to October) precipitation for the area was 341mm, 661mm, and 821mm in 2001, 2002, and 2003, respectively. Long-term average (1971 to 2000) growing precipitation (April to October) for the area was 719 mm. Dominant grass species include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Nash), Indian grass (*Sorghastrum nutans* Nash), and switchgrass (*Panicum virgatum* L.).

Experimental design

We chose 4 management units within the TGPP that varied in size from 400 to 900 ha. We randomly selected management units (n = 2) that were divided into 6 approximately equal area patches as patch treatments (Fuhlendorf and Engle 2004). These management units had exterior fences, but no dividing fences between the patches. We conducted prescribed burns in spring (March) and autumn (August - December) on discrete patches within patch treatment management units (average patch size 100 ha) annually (2001 to 2003) (Table 1, Figure 1), thus each patch in the patch treatment was burned on a 3-year return interval. Recently burned patches received heavy use by cattle, thus creating patches with focal disturbances within the patch treatment. Patches that had not been recently burned were not heavily used by cattle, allowing recovery of vegetation. This shifting of focal disturbance resulted in a mosaic of recently burned patches, recovering patches, and unburned patches that we lumped into categories according to time since focal disturbance in the patch treatment (Table 1). Unburned patches were those patches in the patch treatment that had not been burned during the study at the time of sampling (Table 1). The remaining management units were

designated as controls (n = 2) in which we conducted annual spring (March) burns uniformly across the management units (Table 1). Even though we uniformly burned the control management units, we arbitrarily divided each unit into 6 patches and designated as "all burn patches" to compare the control or "traditional treatment" with the patch treatment at a patch level. A single exterior fence enclosed each management unit in the traditional treatment. The traditional treatment, used over the vast majority of the Flint Hills region (Robbins and Ortega-Huerta 2002), consisted of annual, complete spring burns (all patches) accompanied with the introduction of livestock from mid-April to mid-July. Cattle were introduced in patch treatment and traditional treatment management units from about 15 April to 20 July at a rate of 1.2 ha/animal. Cattle had free access to all patches within each management unit, so cattle could choose between burned and unburned patches in the patch treatment. Cattle chose to graze burned areas in the patch treatment, thus stocking density (number of cattle/grazed area) on burned patches in the patch treatment was roughly 3 times the stocking density in the traditional treatment.

Field methods

Grassland Birds

We estimated abundance of breeding birds in each patch within replicate management units using a point count method during spring of 2001 to 2003 (15 May to 1 July); (Ralph et al. 1993). Point counts result in indices of bird abundance that can be used to test for differences in the abundance of a given bird species among patch types and treatments. We established 100-m radius point counts evenly spaced within each management unit to determine the abundance of birds by species (Ralph et al. 1993). All

point counts were 300 m apart and 150 m from fences or roads. Each management unit (n = 4) contained 6 patches, and each patch contained 4 point counts evenly spaced, or 24 point counts/management unit (Figure 1). All point counts were observed 4 times, beginning 15 May to 30 June. Observers recorded all bird species seen or heard within each 100-m radius point count for 10 minutes after arriving at the point count location. Point counts were located with a handheld GPS unit accurate to +/- 5 m. Observers alternated points and order of points between sessions to avoid bias. Counts were not conducted during periods of heavy rain or wind > 8 km/hour. Each point count was conducted between 0630 and 1030 hours CDT. Most birds were identified by song, but binoculars (10X) were used to verify bird identification when necessary.

Vegetation

Vegetation composition and structure were measured in 2 sampling sessions concurrent with bird point counts, once during the early growing season (mid-May) and about 1 month later, to monitor within-growing season changes in habitat structure that may be related to bird abundance. At each point count location, we measured canopy cover of plant functional groups (tallgrass, shortgrass, grasslike, forb, shrub), cover of bare ground and litter, and vegetation structure (vegetation height, angle of obstruction) to determine treatment effects. We sampled vegetation composition and structure in 0.10 m^2 quadrats centered on each point count location (5 quadrats 20 m apart on a line in 4 cardinal directions from the center of each point count; (20 plots/point); (Figure 1); (Daubenmire 1959). Vegetation height (cm) and angle of obstruction (°), measurements of vegetation structure (Harrell and Fuhlendorf 2002), were recorded at the back, left corner of each quadrat.

Statistical analysis

Structure of the grassland bird community and vegetation functional groups at the patch-level were subjected to an indirect gradient analysis, Detrended Correspondence Analysis (DCA) using default options with PCORD software (Jongman et al. 1987, Fuhlendorf and Engle 2004). DCA has been used to summarize general similarities and differences among grassland bird communities and can quantify compositional dynamics over time (Collins 2000). We averaged point counts within patches (4 point counts/patch) for bird abundance and vegetation data to evaluate the effect of patch treatment on vegetation and the grassland bird community. DCA separated sites based on total environmental variation, so we used the range of DCA site scores and the standard deviation among patches within a management unit for tallgrass, forb, litter, bare ground, height, and angle of obstruction to assess patch-level heterogeneity. We used correlations to decipher relationships between the DCA for the vegetation data and the DCA for the bird data, and to interpret DCA axes gradients.

We also computed mean and standard errors of vegetation composition and structure and abundance of grassland bird species within patches. Our objective was to investigate change in the grassland bird community, only bird species within the grassland bird guild and those known to extensively use grasslands were included (Zimmerman 1993, 1997). We excluded greater prairie chicken (*Tymapanuchus cupido*) from the analyses because their secretive nature and low density made detection using point count methods difficult.

RESULTS

Vegetation Functional Groups

Vegetation differed minimally between sampling sessions (Figures 2 and 3). The first two axes of the DCA for session 1 accounted for 53% of the variance in the data. DCA axis 1 and 2 for session 1 had eigenvalues of 0.332 and 0.054, respectively. The first two axes of the DCA for session 2 also accounted for 53% of the variance in the data. DCA axis 1 and 2 for session 2 had eigenvalues of 0.326 and 0.041, respectively. On DCA axis 1 for session 1 and 2, the order of influence of functional group variables based on the species loading scores was litter, grasslike, tallgrass, and bare ground (Figures 2a and 3a). For DCA axis 2 for both sessions, the order of influence of functional group variables based on the species loading scores was shrub, shortgrass, grasslike, and litter (Figures 2a and 3a). DCA axis 1 site scores and time since focal disturbance were correlated ($r = 0.90$ for session 1 and $r = 0.88$ for session 2). Thus, patches in both sessions were arranged along axis 1 by a gradient of time since focal disturbance.

The range of patch site scores along DCA axis 1 within a treatment was an indicator of spatial and temporal variability or heterogeneity because it described the diversity in vegetation functional group composition among patches. The range of site scores across all patches and years for DCA axis 1 in the patch treatment was 18 to 173 and 39 to 173 for session 1 and 2, respectively (Figures 2b,c and 3b,c). In comparison, the range of site scores across all patches and years for DCA axis 1 in the traditional treatment was 49 to 74 and 61 to 89 for session 1 and 2, respectively (Figures 2b,c and 3b,c). Thus, variability was 5.5 times greater in the patch treatment compared with the

traditional treatment, indicating greater vegetation heterogeneity in the patch treatment. Heterogeneity (standard deviation among patches) of tallgrasses and bare ground in the patch treatment increased after the initial year of the study and maintained higher variability than the traditional treatment for the duration of the study for both sessions of sampling (Table 2). Heterogeneity in litter among the patches was as much as 40 times greater in the patch treatment than the traditional treatment during the study (Table 2). Changes in the traditional treatment consisted primarily of an increase in tallgrass cover and a decrease in forb and bare ground cover over the 3 years of the study (2001 to 2003), which can be attributed to a 2.4 fold increase in growing season precipitation (Table 3).

Cover of functional groups varied among years, within years, and between treatments (Table 3). Bare ground increased and tallgrass and litter cover decreased in the patch treatment after focal disturbance (<13 months) (Figure 2a, 3a, 4). In the DCA for session 1 and 2, patches in the patch treatment shifted toward the right with increasing time since focal disturbance, regardless of year (Figures 2c and 3c). That shift reflected increasing cover of tallgrass and litter with increasing time since focal disturbance in the patch treatment (Figures 2a, 3a, 4). Tallgrass cover was similar among years and between treatments (Table 3). Litter cover was greater in the patch treatment than in the traditional treatment for all years (Table 3). Annual spring fire eliminated nearly all litter cover in the traditional treatment, whereas litter was eliminated in patches with recent focal disturbance (<13 months) in the patch treatment. Litter accumulated rapidly as patches recovered from focal disturbance (>13 months) in the patch treatment (Figure 4). Bare ground decreased with increasing time since focal disturbance in the patch treatment.

Bare ground in the traditional treatment was lower than bare ground in patches with recent focal disturbance (<13 months) within the patch treatment. In contrast, bare ground was higher in the traditional treatment than bare ground in recovering patches (>13 months) within the patch treatment (Figure 4). Differences in bare ground at the patch level between treatments occurred because the traditional treatment was completely burned annually, while burns in the patch treatment were limited to one-third of each management unit annually.

Several patches in the patch treatment that had a focal disturbance 13- to 36 months before sampling had a similar functional group composition to patches that had not been burned in >2 years prior to the beginning of the study (unburned), indicating a recovery of vegetation to pretreatment levels (Figures 2c, 3c and 4). Patches burned in spring and autumn differed little in ordination space, indicating burn season had a relatively small influence on functional group composition in the patch treatment (Figures 2b,c and 3b,c, Table 3).

Vegetation Height and Angle of Obstruction

Vegetation structure varied among years, within years, and between treatments (Table 3). Vegetation height was greater in the patch treatment than the traditional treatment (Table 3, Figure 5). In the patch treatment, height increased with increasing time since focal disturbance (Figure 4). Vegetation height in the traditional treatment was greater than height in patches with recent focal disturbances (<13 months) in the patch treatment, and lower than in recovering patches in the patch treatment (>13 months) (Figure 4). Angle of obstruction was not significantly different between the patch and traditional treatments in 2002 to 2003 (Figure 5). Angle of obstruction was lower in the

recently burned patches within the patch treatment than in the recovering patches within the patch treatment or the traditional treatment (Figure 4). Structural heterogeneity, based on height and AOB, was also greater at the patch level in the patch treatment than the traditional treatment (Figure 5). Heterogeneity in height was 5 times greater in the patch treatment than the traditional treatment throughout the study (Figure 5). Heterogeneity in AOB was 2 to 4 times greater in the patch treatment than the traditional treatment throughout the study (Figure 5).

Grassland Birds

Point count data were averaged to patch level (4 point counts/patch). The first two axes of the DCA accounted for 35% of the variance in the data. DCA axis 1 and 2 had eigenvalues of 0.149 and 0.034, respectively. On DCA axis 1, the most important bird species were Henslow's sparrow, mourning dove (*Zenaida aurita*), upland sandpiper, and dickcissel (Figure 5aa). For DCA axis 2, the most important bird species were lark sparrow, redwinged blackbird (*Agelaius phoeniceus*), common nighthawk (*Chordeiles minor*), and mourning dove (Figure 5a). Correlation between DCA axis 1 site scores and time since focal disturbance was $r = 0.90$; thus, axis 1 separation of the grassland bird community was a gradient of bird species response to time since focal disturbance. The range of patch site scores in DCA axis 1 was an indicator of spatial and temporal variability or heterogeneity in the grassland bird community. The range of site scores across all patches and years for DCA axis 1 in the patch treatment was 0 to 131 (131) (Figure 5b,c). The range of site scores across all patches and years for DCA axis 1 in the traditional treatment was 40 to 73 (33) (Figures 6b,c). Thus, variability was 4 times greater in the patch treatment compared with the traditional treatment, indicating greater

heterogeneity in the patch treatment, which was primarily due to time since focal disturbance (Figure 5c). The range of DCA axis 1 scores in the traditional treatment was restricted to the intermediate portion of the range occupied by the DCA axis 1 scores in the patch treatment, indicating the range of the grassland bird community in the traditional treatment was confined within the bounds of the grassland bird community in the patch treatment.

Abundance of mourning dove, upland sandpiper, and killdeer (*Charadrius vociferus*) increased in recent focal disturbances (<13 months) in the patch treatment (Figure 5a, 6). Patches with recent focal disturbance (<13 months) in the patch treatment had higher abundances of these species than the traditional treatment (Figure 6). Upland sandpiper abundance was 5 times greater in patches with recent focal disturbance (<13 months) compared with the other patches in the patch treatment and 2.5 times greater in patches with recent focal disturbance (<13 months) in the patch treatment than the traditional treatment (Figure 6). Lark sparrows were not encountered in patches with 25 to 36 months of recovery or unburned patches in the patch treatment (Figure 6). Patches in the patch treatment shifted toward the right with increasing time since focal disturbance (i.e., recovery), regardless of year (Figure 5c). This shift indicated an increasing abundance of Henslow's sparrow and dickcissel with increasing time since focal disturbance (Figure 5a, 6). Dickcissel abundance was lower in the traditional treatment than in unburned patches within the patch treatment (Figure 6). Henslow's sparrows were not encountered in patches with recent focal disturbance (<13 months) in the patch treatment or in the traditional treatment (Figure 6). Eastern meadowlark reached peak abundance in patches in the intermediate recovering stages (13 to 36 months) in the

patch treatment and reached the lowest abundance in patches with recent focal disturbance (<13 months) in the patch treatment (Figure 6).

Compared with the traditional treatment, the bird community in the patch treatment was more variable, and the Henslow's sparrow in the patch treatment was not encountered in the traditional treatment (Figure 5 and 6). Several grassland bird species that occurred in peak abundance in patches with recent focal disturbance (<13 months) in the patch treatment, such as upland sandpiper, mourning dove, and killdeer, also increased the bird community heterogeneity in the patch treatment compared with the traditional treatment. Patches burned in spring and autumn differed little in ordination space, indicating burn season had a relatively small influence on composition of the grassland bird community in the patch treatment.

Relationships between Vegetation and the Grassland Bird Community

The range of DCA axis 1 site scores was greater in the patch treatment than the traditional treatment in the vegetation and bird analyses, indicating that increased vegetation heterogeneity in the patch treatment led to increased heterogeneity of the grassland bird community. Variability in vegetation and grassland bird community on DCA axes 1 of the patch treatment was primarily driven by time since focal disturbance (Figures 2c, 3c, 6c). DCA site scores from the vegetation analysis were strongly correlated with the DCA site scores from the grassland bird community analysis, indicating that changes in cover of vegetation functional groups cover associated with time since focal disturbance were correlated with changes in the grassland bird community (Figure 7a). On axis 1 of the vegetation DCA, litter was the most important functional group variable, increasing from near 0% cover in patches with recent focal

disturbance (<13 months) in the patch treatment and in the traditional treatment to near 100% cover in patches with >24 months of recovery in the patch treatment (Figure 4). Increases in litter cover over time in the patch treatment were highly correlated with changes in the grassland bird community (Figure 7b). For example, Henslow's sparrow was not present in patches with recent focal disturbance (<13 months) in the patch treatment or the traditional treatment where litter cover was low (Figure 6).

DISCUSSION

Spatial heterogeneity in tallgrass prairie can be increased with patch applications of fire and subsequent grazing compared with uniform applications of fire and grazing. Spatial pattern of disturbance combined with frequency of disturbance influenced vegetation structure and the grassland bird community. Increased spatial heterogeneity provided greater breadth of vegetation structure, increasing habitat diversity available for grassland birds. The role of patchiness, or heterogeneity has been acknowledged in the maintenance of productivity and biodiversity in numerous ecosystems (Collins 1992, Adler et al. 2001, Fuhlendorf and Engle 2001, Benton et al. 2003). Changes in spatial heterogeneity can alter habitat diversity, potentially influencing all groups of species within an ecosystem (Wiens 1974, Adler et al. 2001). Spatial heterogeneity on a landscape can results from edaphic factors or spatially discrete disturbances that create a shifting mosaic (i.e., fire-grazing model); (Fuhlendorf and Engle 2001).

Fire and herbivore grazing have long been identified as essential ecological processes in the maintenance of grassland ecosystems (Collins 2000, Fuhlendorf and Engle 2001, Harrison et al. 2003); however, these disturbances generally have been applied uniformly on the landscape to minimize spatial variability. Our study indicates

that spatial patterns associated with complex disturbance regimes can have important conservation implications. For example, specific studies of grassland birds have noted that coexisting bird species with highly variable habitat requirements are declining rangewide (Askins 2000). Grassland bird species encountered in our study had habitat preferences ranging from heavily disturbed grassland patches (i.e. upland sandpiper) to undisturbed grassland patches (i.e. Henslow's sparrow). Management toward the middle (i.e., moderate, uniform disturbance resulting in homogenous vegetation structure) has traditionally been practiced in grassland management and could be partly responsible for precipitous declines in these and other grassland birds (Knopf 1994, Fuhlendorf and Engle 2004).

Grassland Disturbance

Fire and grazing on grasslands have been studied extensively; however, the effects of those disturbances generally have been considered in isolation, with little investigation of their interactions (Kucera and Koelling 1964, Collins 1987). Recent investigations argue that grasslands developed under the complex interaction of fire and grazing, and that interaction may be a more important determinant of grassland structure than individual disturbances (Collins 1987, Fuhlendorf and Engle 2001).

Fire frequency and seasonality are important factors dictating plant species composition and diversity in grasslands (Kucera and Koelling 1964, Abrams et al. 1986, Hobbs and Huenneke 1992, Collins et al. 1995). Tallgrass prairie typically is burned in the late dormant season, which generally increases matrix-forming perennial grasses and decreases annual grasses and forbs (Abrams et al. 1986, Collins 1987).

Grazing, in contrast to frequent fire, decreases cover of matrix-forming perennial grasses and increases abundance of annual grasses and forbs in tallgrass prairie (Collins 1987). As with fire, intermediate levels of grazing often produce maximum plant species diversity, particularly in ecosystems with a long evolutionary history of grazing (Milchunas et al. 1988, Hobbs and Huenneke 1992).

Spatial pattern of grazing is rarely uniform in grasslands, and the spatial pattern of disturbance is critical for biodiversity. Ungulates tend to graze in areas previously grazed or burned and avoid previously ungrazed or unburned areas, creating a patchwork of disturbed and undisturbed areas (Collins 1987, Hobbs and Huenneke 1992). This behavior can accentuate fine-scale patchiness in grassland ecosystems, creating open spaces for plant recruitment and establishment. However, when grazing pressure is high, forage limitations may outweigh grazing behavior and result in lowered heterogeneity (Fuhlendorf and Engle 2004).

Grazing and fire interact in mesic grasslands, influencing plant communities differently than the individual effects of the disturbances. Experiments in tallgrass prairie have demonstrated that fire alone lowers plant species diversity, but fire and grazing collectively increase diversity more than grazing alone (Collins 1987). Several authors have suggested that species diversity in a given ecosystem will be greatest under disturbance regimes that most closely mimic the historical regime under which the ecosystem evolved (Hobbs and Huenneke 1992, Fuhlendorf and Engle 2001). This idea appears to be valid in mesic grasslands of North America including our study site. These grasslands evolved under the interactive influence of fire and grazing, with bison grazing often occurring in recently burned areas (Coppedge and Shaw 1998, Fuhlendorf and

Engle 2001). Our patch treatment was designed to simulate historical interactions of fire and grazing in tallgrass prairie by applying the fire-grazing model (Fuhlendorf and Engle 2001) and demonstrated that spatial pattern of the fire-grazing interaction may be the most important factor in describing effects of disturbance on grassland heterogeneity and biodiversity.

Bird response to vegetation change

Grassland bird response to our treatments mirrored that of vegetation response, with 4 times greater avian heterogeneity in the patch treatment than the traditional treatment, demonstrating the strong association between grassland birds and vegetation. Litter, which was the most heterogeneous vegetation variable in the patch treatment, was strongly correlated with variability in the grassland bird community as indicated by the DCA site scores. Henslow's sparrow was absent in the traditional treatment and patches in the patch treatment with recent focal disturbance, due to lack of litter accumulation. Other studies from the tallgrass prairie have reported that changes in animal communities (breeding birds, grasshoppers, and small mammals) were not associated closely with changes in plant communities (Collins 2000). However, a recent review of studies from 1960 to 2003 relating habitat heterogeneity to animal diversity across numerous ecosystems and species groups found that 85% of studies demonstrated a positive relationship between habitat heterogeneity and animal diversity (Tews et al. 2004). One reason for inconsistency between studies is that species composition changes in the plant community may not accurately reflect changes in habitat structure and heterogeneity that dictate grassland bird response (Collins 2000, Chapman et al. 2004). Our study measured plant functional group changes, which are more indicative of habitat structure that

influences grassland bird habitat selection than plant species composition changes (Chapman et al 2004). Structural complexity is often more important in defining animal diversity than plant species diversity or composition (Pianka 1967, Chapman et al. 2004, Tews et al. 2004).

In our study, fire and grazing interacted to create patches of focal disturbance that were more severely disturbed in terms of vegetation structure than traditional management regimes. Other studies have examined effects of individual, spatially homogenous disturbances. Focus on spatially uniform disturbances and ignoring disturbance pattern and scale may lead to poorly described disturbance-diversity hypotheses (Huston 1994, Collins et al. 1995, Bestelmeyer et al. 2003). Additionally, studies of relationships between plant and animal communities in grasslands generally have not examined the range of disturbance intensities found in our study and, as a result, may not have detected as strong of a relationship between vegetation and animal species. In our patch treatment, high disturbance intensity (i.e., patches burned followed by intense grazing) combined with intermediate disturbance frequency and extent (3-year fire return interval on individual patches within a unit) created a wide range of habitat structure. The fact that some characteristic grassland bird species occurred in greatest abundance within focally disturbed patches while others occurred in relatively undisturbed patches in our patch treatment suggests that a similar background range of disturbance intensities within a shifting mosaic occurred within the evolutionary history of tallgrass prairie ecosystems. Conservation efforts should focus on understanding interactions between disturbance extent, frequency, and intensity to better describe patterns in grassland diversity.

Shifts in abundance of dominant species, decreased spatial heterogeneity, and lowered species richness have been associated with uniform applications of disturbance in tallgrass prairie ecosystems (Collins et al. 1995, Collins 2000, Fuhlendorf and Engle 2001). For example, management for cattle production near our study area used annual, dormant season fires combined with a short, intensive grazing period in an attempt to maximize livestock production while minimizing long-term site degradation (Launchbaugh and Owensby 1978). This management model has been used in this region for >25 years, and declines in native biota such as prairie grouse have already been associated with the practice (Applegate et al. 2002, Robbins and Ortega-Huerta 2002). Other studies in tallgrass prairie have noted a loss of characteristic prairie forbs under annual spring fire regimes (Kucera and Koelling 1964, Collins 1987). Studies from other continents also have noted incidents of declines in biodiversity associated with annual fire regimes in grasslands (Jansen et al. 1999, Peet et al. 1999).

Temporal and spatial scales of fire and grazing interactions before pre-European settlement of grasslands were likely different than those imposed in our patch treatment. Nonetheless, grassland bird heterogeneity was related positively to increased spatial heterogeneity of vegetation at a patch level in our experiment, indicating the potential importance of heterogeneity as a theoretical and management model for conservation. The success of our model in enhancing grassland bird biodiversity may in part be due to the scale at which we applied the grazing-fire interactions. Many grassland birds require a minimum habitat area as large as 200 ha to maintain viable populations (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999). Our study area had large management units (average 600 ha) and patch sizes (average 100 ha), which were within the minimum

area requirements suggested by past research for the grassland bird species considered in our study. Our patches were also surrounded by a landscape of uncultivated native grassland, whereas past research on area requirements of grassland birds has generally been conducted in the context of fragmented grassland landscapes (Herkert 1994, Vickery et al. 1994). Increasing heterogeneity at a finer scale (i.e. smaller patches) may not be effective in increasing biodiversity, particularly if the scale of heterogeneity is different than species specific area requirements. In fact, at some scales heterogeneity may actually act as a fragmentation agent from the organism's perspective, potentially reducing biodiversity (Tews et al. 2004). We believe that agricultural uses such as grazing and conservation can be compatible if evolutionary history of the ecosystem, requirements of native fauna, and heterogeneity are considered when developing management regimes.

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Table 1. Burn schedule for patch and traditional treatments at the Tallgrass Prairie Preserve, northcentral OK. M indicates months since patch was burned.

	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5	Patch 6
Patch						
2001	Burned	Burned	Unburned	Unburned	Unburned	Unburned
2002	13-24 M	13-24 M	Burned	Burned	Unburned	Unburned
2003	25-36 M	25-36 M	13-24 M	13-24 M	Burned	Burned
Traditional						
2001	Burned	Burned	Burned	Burned	Burned	Burned
2002	Burned	Burned	Burned	Burned	Burned	Burned
2003	Burned	Burned	Burned	Burned	Burned	Burned

Table 2. Heterogeneity of tallgrass, forb and litter cover, bare ground, height, and angle of obstruction stratified by year, sampling session, and treatment (traditional and patch). Heterogeneity is measured as the standard deviation among patches within a single management unit. Standard error (+/-) of heterogeneity is in parentheses.

Variable	2001				2002				2003			
	Session1		Session2		Session1		Session2		Session1		Session2	
	Trad.	Patch	Trad.	Patch	Trad.	Patch	Trad.	Patch	Trad.	Patch	Trad.	Patch
tallgrass (%)	7.6 (3.7)	12.7 (2.3)	10.1 (5.2)	13.5 (3.9)	5.5 (2.1)	19.9 (0.6)	5.1 (2.2)	13.8 (0.3)	8.8 (1.4)	19.3 (1.1)	6.5 (2.2)	18.7 (4.6)
forb (%)	4.7 (0.6)	5.7 (0.03)	5.5 (1.7)	7.7 (0.1)	3.8 (1.3)	7.0 (1.5)	5.0 (0.7)	9.5 (3.9)	3.1 (0.7)	5.9 (2.6)	4.2 (0.5)	9.2 (4.2)
litter (%)	3.9 (2.3)	43.1 (0.8)	1.6 (0.9)	45.8 (0.2)	0.4 (0.3)	43.2 (1.3)	0.1 (0.1)	44.2 (1.6)	0.1 (0.1)	38.9 (3.0)	0 (0)	42.5 (0.2)
bare ground (%)	7.1 (2.0)	13.6 (5.0)	6.3 (3.1)	9.5 (2.2)	3.2 (0.1)	18.1 (0.2)	4.6 (2.5)	9.7 (0.2)	6.8 (2.1)	21.3 (3.5)	4.0 (1.7)	15.8 (6.0)
height (cm)	1.4 (0.6)	10.3 (0.2)	3.2 (0.9)	11.3 (1.1)	1.6 (0.3)	8.9 (0.2)	3.5 (1.1)	10.8 (1.1)	2.2 (0.2)	9.5 (0.4)	2.9 (1.4)	11.6 (0.3)
angle of obstruction (°)	6.3 (0.5)	11.9 (1.1)	5.5 (2.6)	8.0 (2.1)	1.3 (0.4)	7.8 (0.3)	1.6 (0.7)	3.4 (1.0)	3.2 (1.2)	9.4 (1.9)	2.5 (1.4)	8.8 (4.3)

Table 3. Percent canopy cover of tallgrass, forb and litter cover, percent bare ground, height, and angle of obstruction stratified by year, sampling session, and treatment. Standard error (+/-) is in parentheses.

Variable	2001				2002				2003			
	Session1		Session2		Session1		Session2		Session1		Session2	
	Trad	Patch	Trad.	Patch	Trad.	Patch	Trad.	Patch	Trad.	Patch	Trad.	Patch
tallgrass (%)	55 (1)	57(4)	74 (5)	68 (1)	66 (9)	49 (3)	78 (5)	65 (3)	68 (1)	61 (7)	78 (3)	70 (5)
forb (%)	28 (2)	27 (2)	26 (2)	28 (2)	16 (1)	17 (1)	15 (2)	21 (3)	10 (1)	13 (4)	15 (4)	17 (6)
litter (%)	6 (1)	59 (2)	1 (1)	62 (1)	1 (0)	40 (5)	0 (0)	35 (4)	0 (0)	52 (6)	0 (0)	56 (2)
bare ground (%)	28 (2)	13 (3)	11 (3)	9 (1)	18 (2)	17 (3)	9 (2)	10 (2)	15 (2)	14 (6)	6 (1)	10 (5)
height (cm)	11 (1)	21 (1)	16 (1)	28 (1)	17 (2)	20 (2)	26 (3)	29 (3)	16 (1)	24 (4)	23 (1)	29 (4)
angle of Obstruction (°)	70 (1)	79 (1)	81 (4)	83 (1)	86 (2)	83 (1)	88 (1)	88 (1)	85 (1)	83 (3)	87 (4)	84 (3)

Figure 1. Spatial layout and sampling design of the patch treatment. The solid line represents a fence that encloses the management unit whereas the dotted lines separate the burned patches, which are unfenced. Free movement of animals was allowed within each management unit. Vegetation sampling was hierarchically nested with sample points (5 per line) arranged on sampling lines (4 per bird sampling point) that overlay bird sampling points (4 per patch) nested within patches (6 per management unit) that are within replicated treatments applied to management units. Management units not receiving patch treatment (traditional) were arranged in similar sampling hierarchies.

Figure 1.

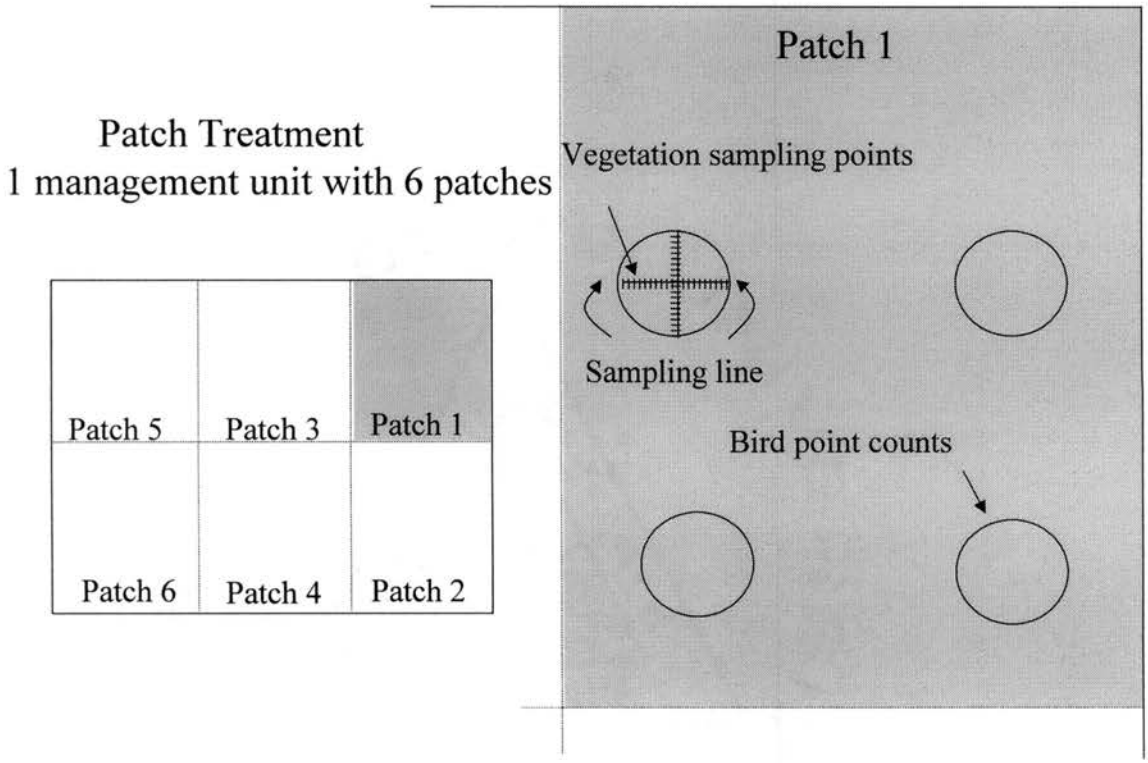

Patch Treatment
1 management unit with 6 patches
Patch 5
Patch 3
Patch 1
Patch 6
Patch 4
Patch 2
Patch 1
Vegetation sampling points
Sampling line
Bird point counts

Figure 2. Plots of the first 2 axes of the detrended correspondence analysis for the vegetation data from sampling session 1 (15 May to 5 June, 2001 to 2003). The plots represent scores for functional groups, bare ground, and litter (a); site (patch) scores for the traditional treatment (b); and site (patch) scores for the patch treatment (c). Envelopes encompass site scores for a given time since focal disturbance. Year symbols indicate year of observation, not year of treatment.

Figure 2.

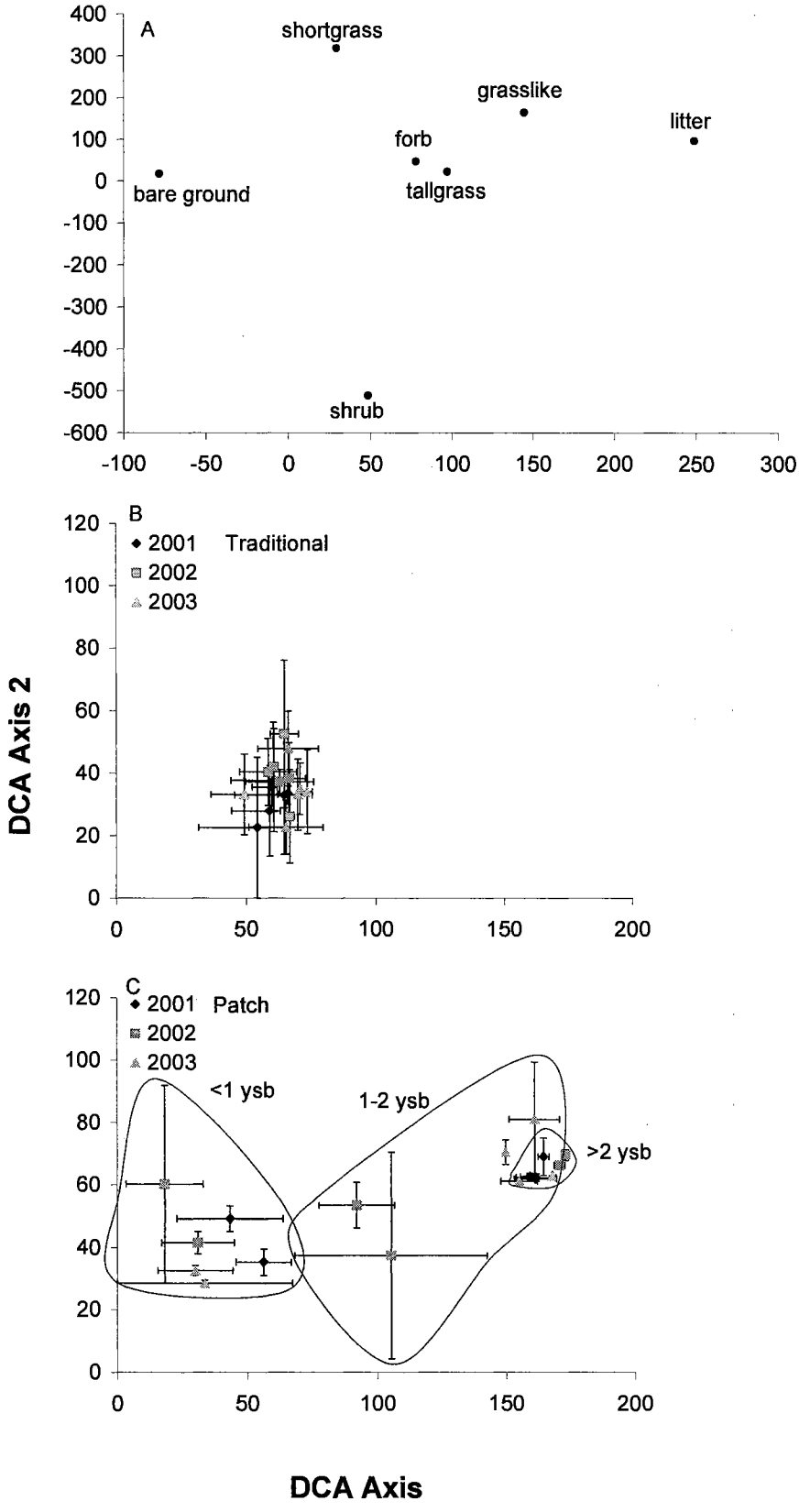

A
shortgrass
grasslike
litter
forb
tallgrass
bare ground
shrub
B
2001 Traditional
2002
2003
C
2001 Patch
2002
2003
<1 ysb
1-2 ysb
>2 ysb
DCA Axis 2
DCA Axis

Figure 3. Plots depicting the first 2 axes of the detrended correspondence analysis for the vegetation data from sampling session 2 (10 June-30 June 2001-2003). The plots represent scores for functional groups, bare ground, and litter (a); site (patch) scores for the traditional treatment (b); and site (patch) scores for the patch treatment (c). Envelopes encompass site scores for a given time since focal disturbance. Year symbols indicate year of observation, not year of treatment.

Figure 3.

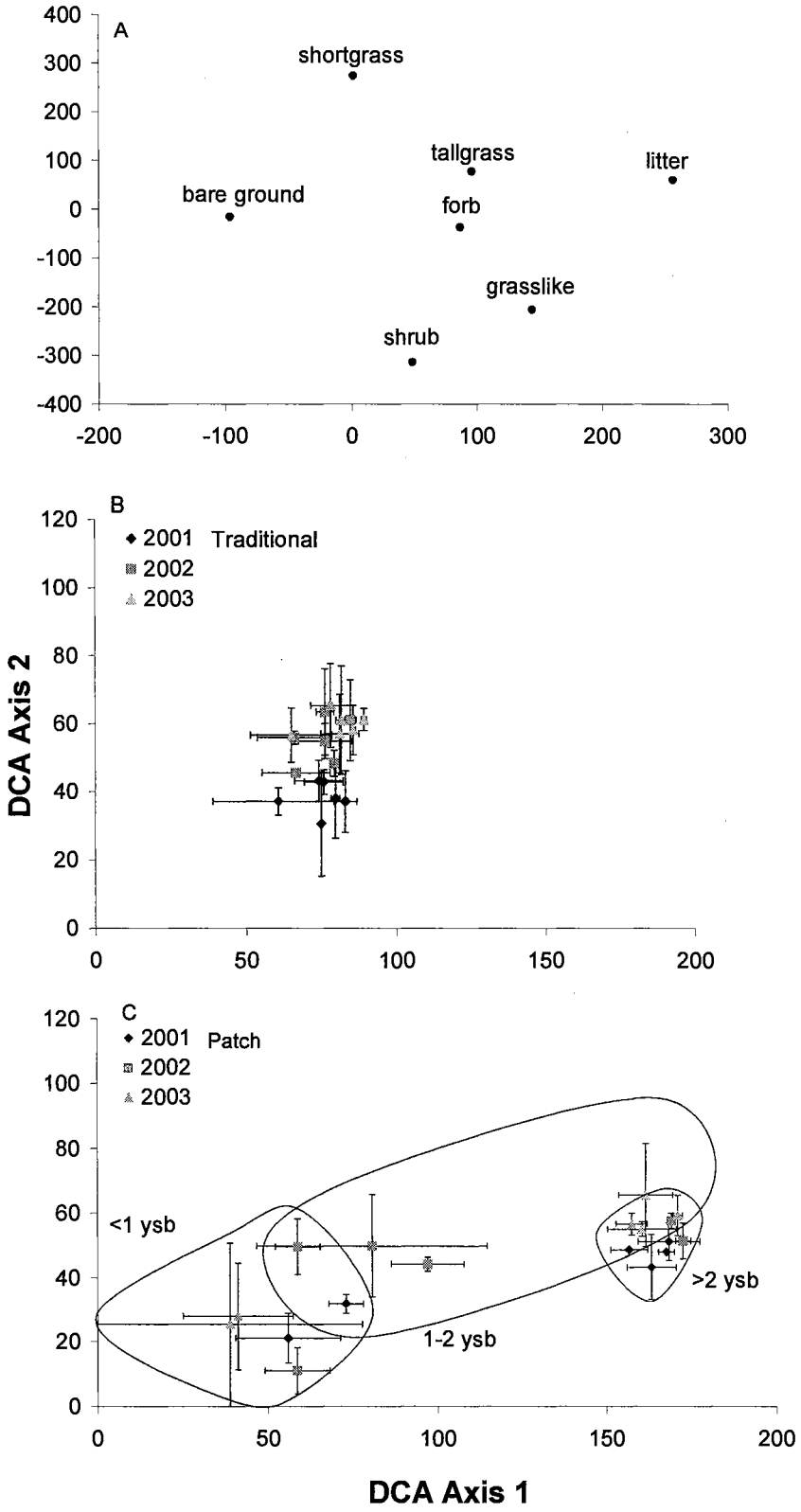

A
shortgrass
tallgrass
litter
bare ground
forb
grasslike
shrub
B
2001 Traditional
2002
2003
DCA Axis 2
C
2001 Patch
2002
2003
<1 ysb
1-2 ysb
>2 ysb
DCA Axis 1

Figure 4. Canopy cover of 2 dominant functional groups, tallgrasses and forbs, and cover of litter and bare ground in patch treatment stratified by months since last focal disturbance (patch treatment) and traditional treatment. Data is from session 1 sampling period (15 May to 5 June, 2001 to 2003).

.

Figure 4.

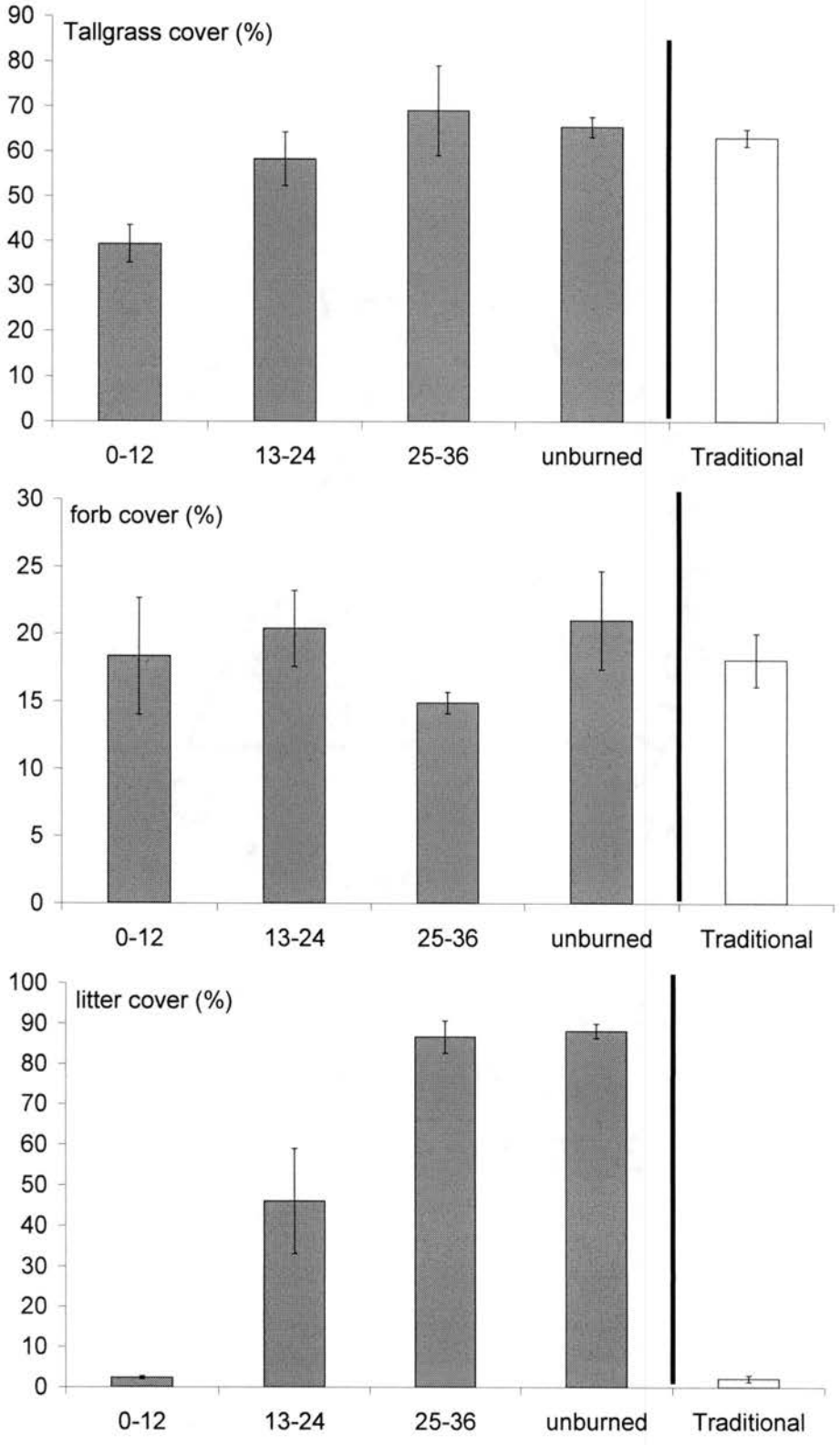

Tallgrass cover (%)
90
80
70
60
50
40
30
20
10
0
0-12
13-24
25-36
unburned
Traditional
forb cover (%)
30
25
20
15
10
5
0
0-12
13-24
25-36
unburned
Traditional
litter cover (%)
100
90
80
70
60
50
40
30
20
10
0
0-12
13-24
25-36
unburned
Traditional
Months since focal disturbance

Figure 4 continued.

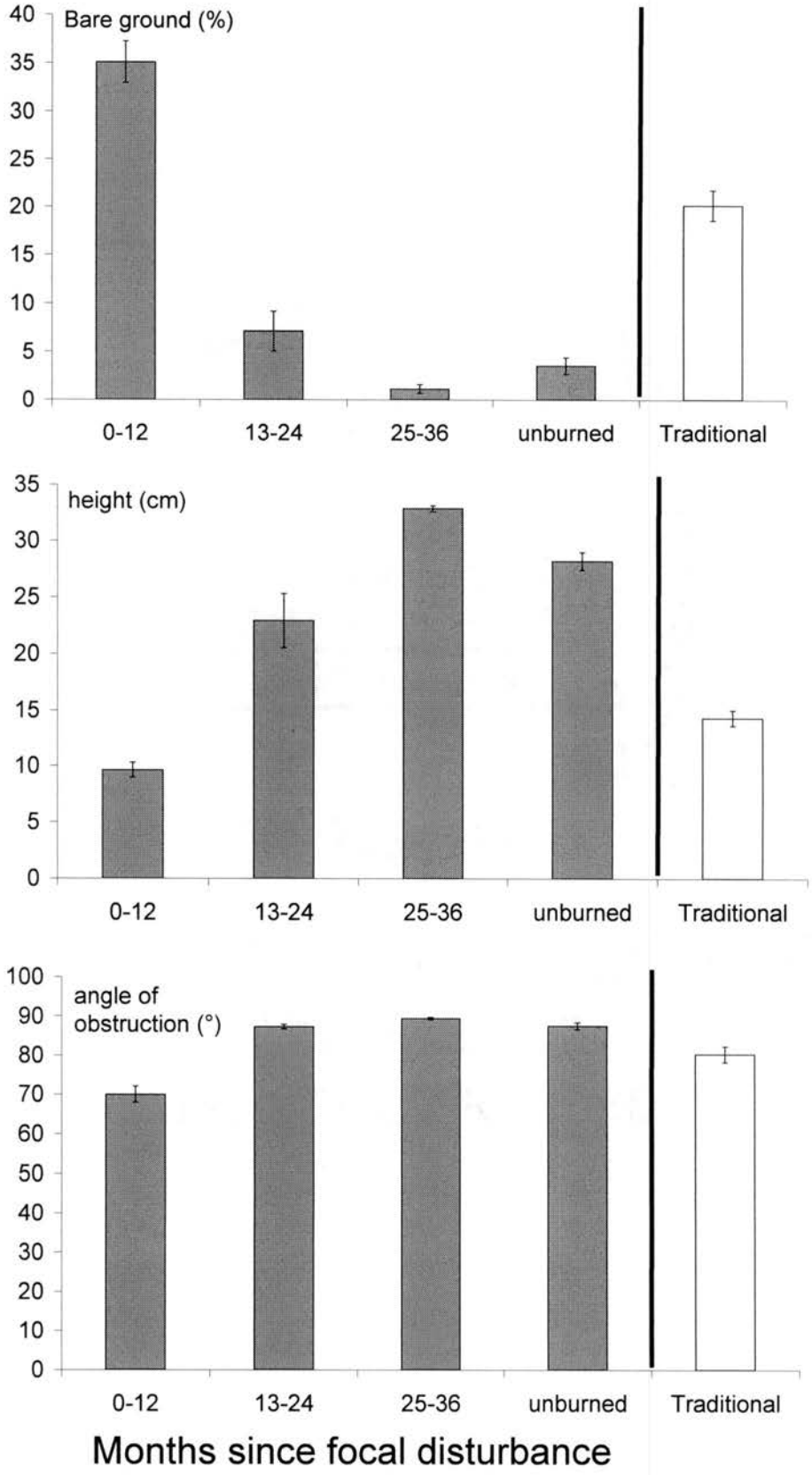


Figure 5. Plots of the first 2 axes of the detrended correspondence analysis for the grassland bird abundance data. The plots represent species scores for functional group and bare ground and litter (a); site (patch) scores for the traditional treatment (b); and site (patch) scores for the patch treatment (c). Envelopes encompass site scores for a given time since focal disturbance. Year symbols indicate year of observation, not year of treatment.

Figure 5.

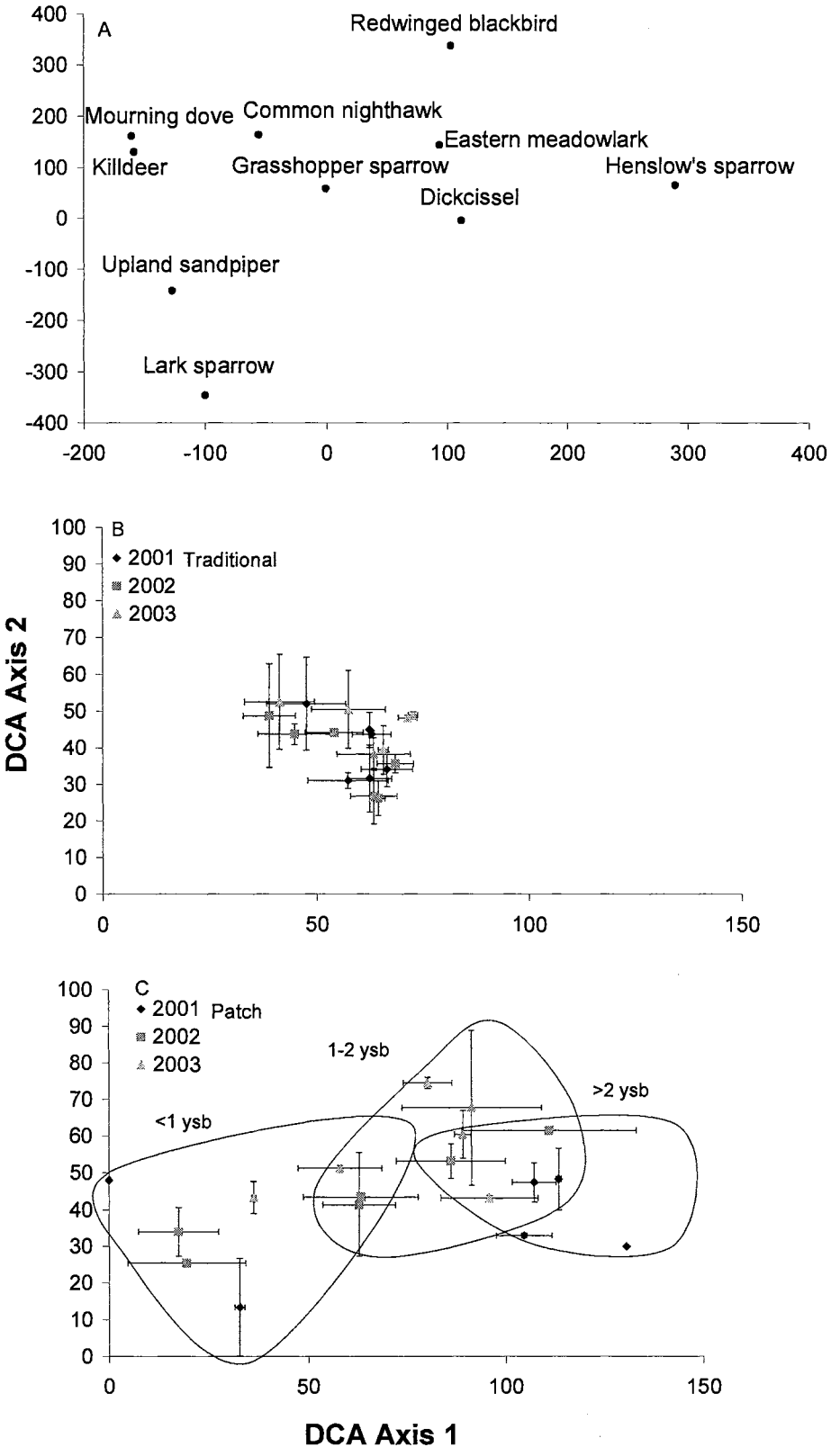

A
Redwinged blackbird
Mourning dove
Common nighthawk
Eastern meadowlark
Killdeer
Grasshopper sparrow
Henslow's sparrow
Dickcissel
Upland sandpiper
Lark sparrow
400
300
200
100
0
-100
-200
-300
-400
-200
-100
0
100
200
300
400
B
2001 Traditional
2002
2003
DCA Axis 2
100
90
80
70
60
50
40
30
20
10
0
0
50
100
150
C
2001 Patch
2002
2003
1-2 ysb
>2 ysb
<1 ysb
DCA Axis 1

Figure 6. Abundance of 10 grassland bird species (#/100 m radius point count) in patch treatment stratified by months since last focal disturbance (patch treatment) and traditional treatment.

Figure 6.

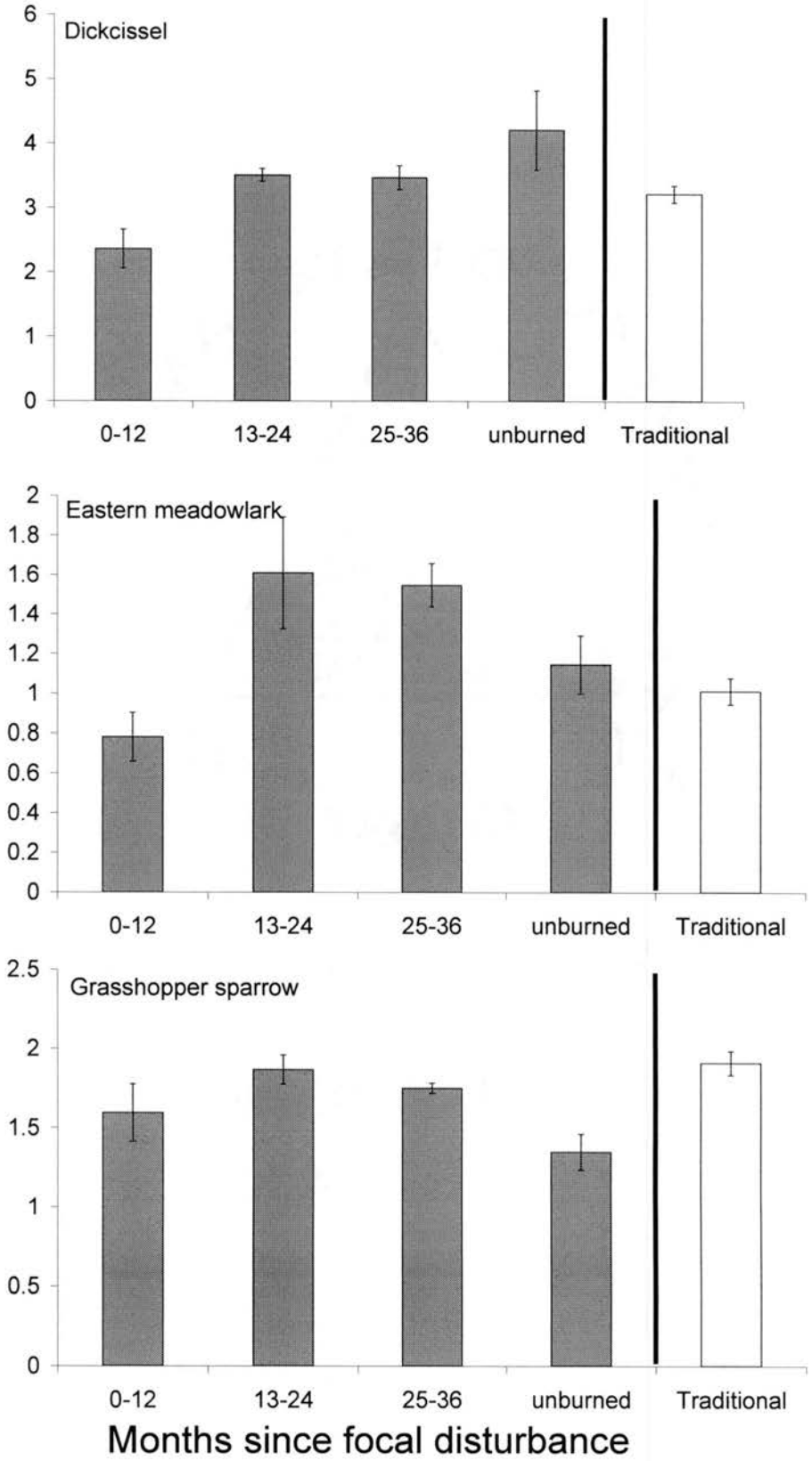

Dickcissel
6
5
4
3
2
1
0
0-12
13-24
25-36
unburned
Traditional
Eastern meadowlark
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0-12
13-24
25-36
unburned
Traditional
Grasshopper sparrow
2.5
2
1.5
1
0.5
0
0-12
13-24
25-36
unburned
Traditional
Months since focal disturbance

Figure 6 continued.

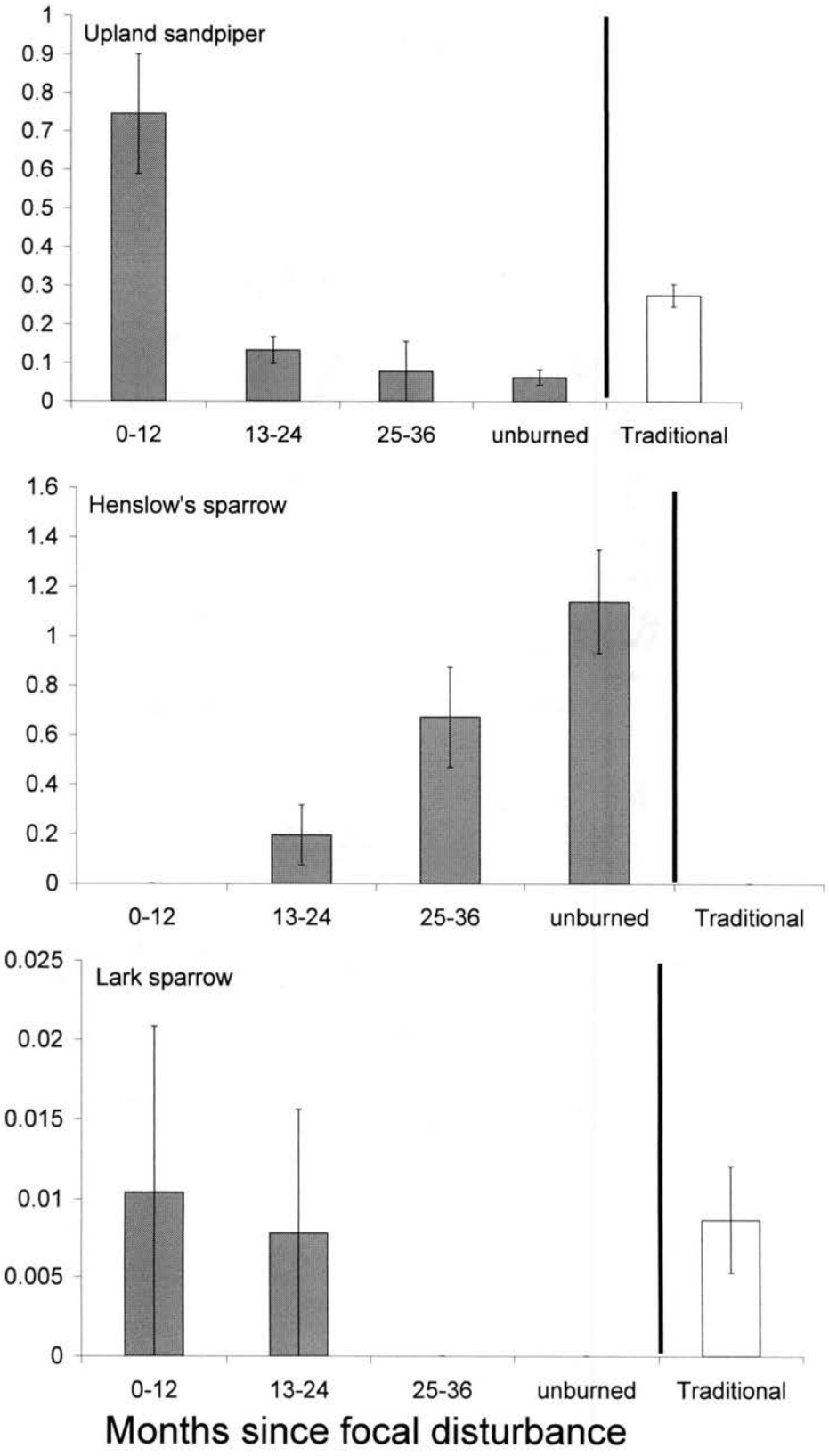


Figure 6 continued.

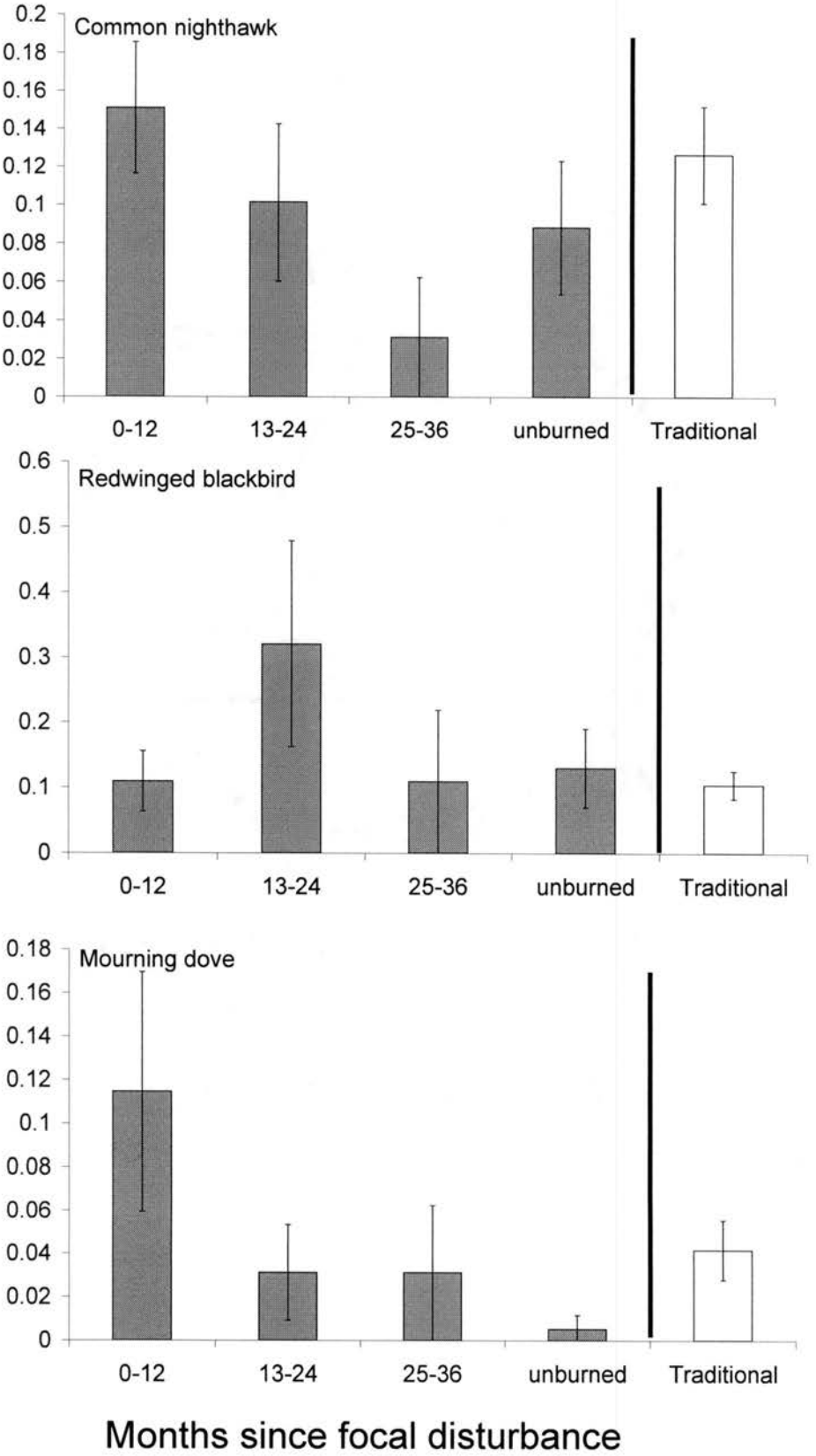


Figure 6 continued.

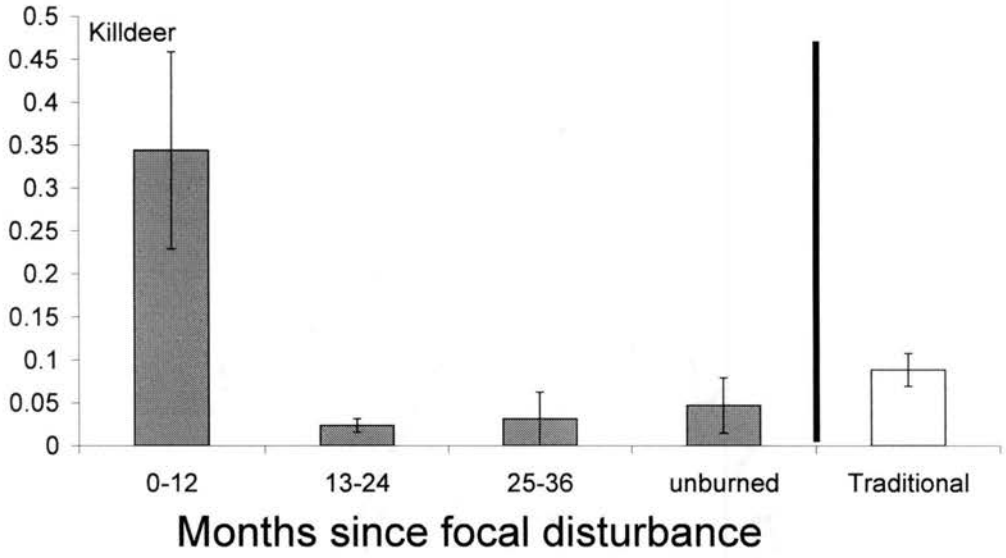
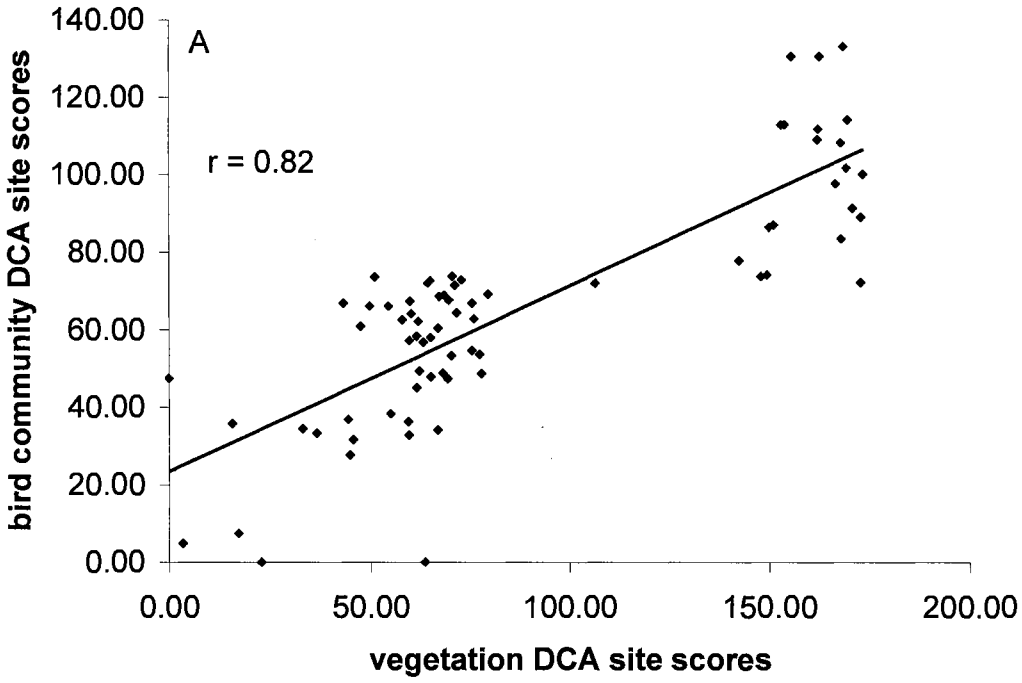
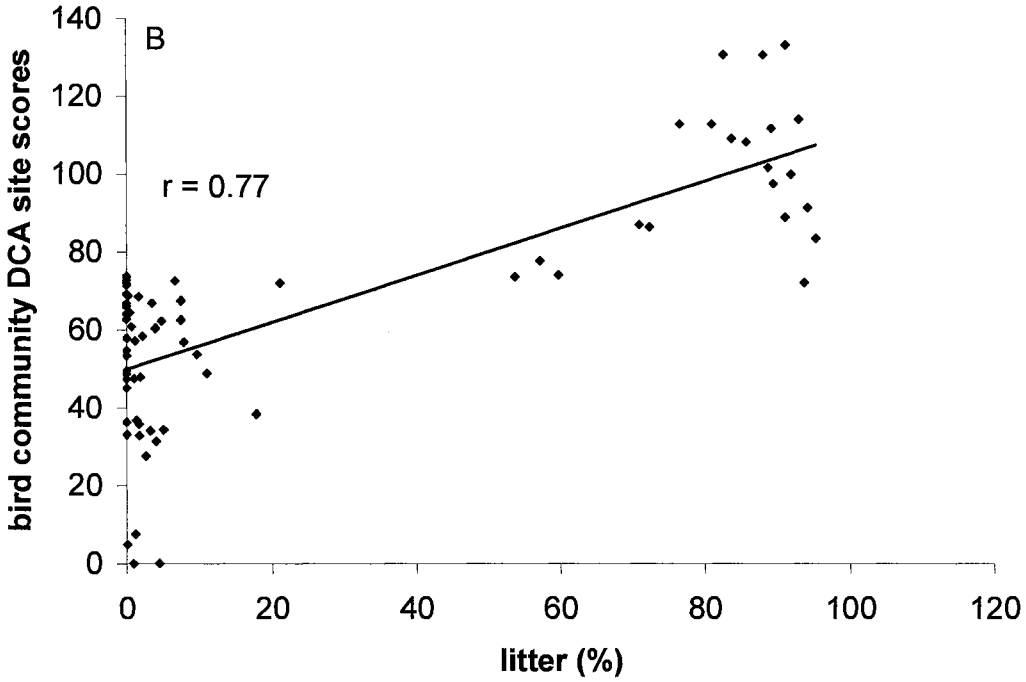


Figure 7. Correlations between (a) grassland bird DCA site scores (patch) and session 1 vegetation DCA site scores (patch) and (b) grassland bird DCA site scores (patch) and litter cover. Data used is from both patch and traditional treatments

Figure 7.


A
r = 0.82
bird community DCA site scores
vegetation DCA site scores
140.00
120.00
100.00
80.00
60.00
40.00
20.00
0.00
0.00
50.00
100.00
150.00
200.00


B
r = 0.77
bird community DCA site scores
litter (%)
140
120
100
80
60
40
20
0
0
20
40
60
80
100
120

CHAPTER 3

MULTISCALE FACTORS INFLUENCING GRASSLAND BIRD COMMUNITY DYNAMICS

ABSTRACT

Grasslands birds are declining at a more rapid rate than any other bird guild in North America. Causal factors for these declines are multi-scaled, including habitat loss and fragmentation, woody plant encroachment, and changes in historic disturbance regimes. We chose study sites within an unfragmented tallgrass prairie landscape with heterogeneity and homogeneity fire–grazing treatments applied. We subsequently developed Poisson regression models that estimated the relative influence of multi-scale habitat factors on the grassland bird community. Our data set consisted of abundances of 10 grassland bird species and landscape and broad-scale habitat variables including patch and traditional treatments, time since focal disturbance and presence of ponds, creeks, rock outcrops woody edge, petroleum structures, and roads as well as fine-scale habitat variables including cover of tallgrass, shortgrass, grasslike, forb, bare ground, litter, shrub, and vegetation height, and angle of obstruction from 288 point count locations over 3 years. Models were developed for each species independent of other species. All broad-scale variables except presence of roads were important for more than one species. Models for (dickcissel *Spiza americana*, redwinged blackbird *Agelaius phoeniceus*, and

northern bobwhite *Colinus virginianus*) were negatively associated with petroleum structures <150 m from the census location. All grassland bird species were influenced by either treatment or time since focal disturbance, which was central to the patch treatment. Our study demonstrates the importance of multi-scale factors such as time since focal disturbance and presence of natural and anthropogenic landscape variables in the structuring of grassland bird communities. We suggest a hierarchical approach to prioritize factors that influence conservation of grasslands and their associated fauna.

Keywords: disturbance, fire, grazing, heterogeneity, petroleum, poisson modeling, tallgrass prairie

INTRODUCTION

Grasslands birds are declining at a more rapid rate than any other bird guild in North America (Sampson and Knopf 1994). Causal factors for these declines are multi-scaled, including habitat loss and fragmentation, encroachment of woody plants on grasslands, and changes in fire and grazing regimes. At broad spatial scales, loss of grasslands combined with fragmentation of remaining grasslands undoubtedly has affected grassland bird populations (Herkert et al. 2003). At intermediate scales, encroachment of woody plants in grasslands can lower grassland bird productivity through increased predation, increased nest parasitism and habitat avoidance (Johnson and Temple 1990, Vickery et al. 1994, O'Leary and Nyberg 2000, Winter et al. 2000, Jensen and Finck 2004). Some anthropogenic landscape features, such as wind turbines, also may act as fragmentation agents in grasslands from a bird perspective, although the causal factors associated with these structures are unclear (Leddy et al. 1999). Within

remaining grasslands, vegetation structure driven by disturbances such as fire and grazing often influences fine-scale habitat selection by grassland birds. Structural heterogeneity of vegetation within grasslands often shapes grassland bird community dynamics (MacArthur and MacArthur 1961, Wiens 1974, Walk and Warner 2000, Chapman et al. 2004, Chapter II), with some bird species selecting grassland habitats with specific vegetation structural characteristics (Cody 1985). This suggests that spatially and temporally variable disturbances in grasslands that maintain landscape-level vegetation heterogeneity are critical to the conservation of the grassland bird community (Askins 2000).

Disturbances such as grazing and fire historically maintained grassland heterogeneity (Knapp et al. 1999, Fuhlendorf and Engle 2001), but current management models have often failed to consider the importance of heterogeneity for biodiversity. Current management of grasslands for agricultural production typically reduces inherent spatial and temporal habitat heterogeneity within landscapes through uniform application of fire and grazing (Holechek et al. 2003). Unfortunately, application of such management models may detrimentally effect biodiversity, particularly in ecosystems that developed under a spatially and temporally dynamic disturbance regime such as the tallgrass prairie of North America (Fuhlendorf and Engle 2004). Declining grassland obligate bird species may be associated partly with management driven reductions in heterogeneity that minimize heavily disturbed and undisturbed plant communities required by some grassland bird species (Knopf 1994).

To further understand grassland bird declines, researchers should strive to understand multi-scale grassland bird habitat associations. This requires a hierarchical

approach to investigating causal factors associated with grassland bird declines. Many investigations in grassland bird habitat associations have been conducted in fragmented grasslands. We chose study sites within an unfragmented tallgrass prairie landscape so we could develop models that estimated the relative influence of multi-scale habitat factors on a grassland bird community. We predict that spatio-temporally variable habitat attributes and semi-permanent landscape features interact to structure grassland bird communities, and conservation efforts for grassland birds should consider the influence of these factors at multiple scales.

METHODS

Site description

We conducted research on the Tallgrass Prairie Preserve (TGPP) in northcentral Oklahoma, USA (36° 50′N, 96° 25′W), owned and operated by The Nature Conservancy. The Preserve lies within the southern portion of the Flint Hills region of the Great Plains and contains one of the last remnant continuous tallgrass prairie landscapes in North America. The climate is temperate, with hot summers (average high of 33.9 C for July 2001-2003) and cold winters (average low of -4.8 C for Jan. 2001-2003). Growing-season (April-October) precipitation for the area was 341mm, 661mm, and 821mm for 2001, 2002, and 2003, respectively. Long-term average (1971-2000) growing precipitation (April-October) for the area was 719 mm. Dominant grass species include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Nash), Indian grass (*Sorghastrum nutans* Nash), and switchgrass (*Panicum virgatum* L.).

Experimental design

We chose 4 management units within the TGPP that varied in size from 400 to 900 ha. Our treatments consisted of a heterogeneous, patch treatment (n = 2) and a homogeneous, traditional treatment (n = 2). Within management units, half of our sampling points were in the heterogeneity treatment and half were in the homogeneity treatment. In the patch treatment, prescribed burns were conducted on one-sixth each management unit in the spring and one-sixth of each management in the autumn of each year, for a 3-year fire return interval. Prescribed burns were conducted in the traditional treatment in the spring of each year, for a 1-year return interval. Cattle were introduced in patch treatment and traditional treatment management units about 15 April at a rate of 1.2 ha/animal and removed about 20 July as is typical livestock management within the region. Refer to Fuhlendorf and Engle (2004) for a more detailed description of patch treatment.

Our analyses included 17 explanatory habitat variables which were split into groups based on relative scale including: 1) broad-scale variables (treatment, time since disturbance, ponds, creeks, rocky outcrops, woody edge, petroleum structures, and roads) and 2) fine-scale habitat variables (cover of tallgrass, shortgrass, grasslike, forb, shrub, vegetation height, and angle of obstruction). Treatments included patch (coded as 1) and traditional (coded as 0); time since focal disturbance included 0, 1, and 2 years since focal disturbance and unburned, pretreatment sites (coded as 3) in the patch treatment and annually burned (coded as 0.5) sites in the traditional treatment. Time since focal disturbance in the traditional treatment was coded as 0.5 since the intensity of disturbance

was intermediate between sites with recent focal disturbance (0) and 1 year since focal disturbance (1) in the patch treatment.

Field methods

Grassland Birds

We estimated abundance of breeding birds in each replicate management unit using a point count method during springs of 2001 to 2003 (15 May to 1 July); (Ralph et al. 1993). Point counts result in indices of bird abundance that can be used to test for differences in the abundance of a given bird species among treatments. We established 100-m radius point counts evenly spaced within each management unit to determine the abundance of birds by species (Ralph et al. 1993). All point counts were 300 m apart, and at least 150 m from fences. Each management unit (n=4) contained 24 point counts. All point counts were observed 4 times, beginning 15 May and ending 30 June each year. Observers recorded all bird species seen or heard within each point count for 10 minutes after arriving at the point count location. Point counts were located with a handheld GPS unit accurate to +/- 5 m. Observers alternated points counted and order of points between sessions to avoid bias. Counts were not conducted during periods of heavy rain or wind exceeding 8 km/hr. Each point count was conducted between 0630 and 1030 hours CDT. Most birds were identified by song, but binoculars (10X) were used to verify bird identification when necessary.

Landscape and Habitat attributes

We measured the from each of our point count locations distance to several landscape attributes including ponds, creeks, rock outcrops, woody edge, petroleum structures, and roads. All ponds and creeks contained water at the time of bird sampling.

Rock outcrops were considered to be any large (>2 m), upright, naturally occurring rocky structure. Woody edge was considered to be any tall (>2 m), continuous woody vegetation, (i.e. shrubs and trees). We considered roads as any graveled or further improved surface > 2 m wide. No roads in our study area were paved or > 15 m in width. All landscape variables < 150 m from our point counts were included in our data set. Landscape variables were the prevailing structural features within our study area. Both of our treatments contained all landscape variables except petroleum structures, which were found only in the patch treatment (table 2).

Vegetation composition and structure were measured during the early growing season (mid-May), concurrent to the collection of bird abundance data. At each point count location, we estimated canopy cover of plant functional groups (tallgrass, shortgrass, grasslike, forb, shrub); (Daubenmire 1959), cover of bare ground and litter, and herbaceous vegetation structure (vegetation height, angle of obstruction) to determine effects of the patch treatments. We sampled vegetation composition and structure in 0.10 m^2 quadrats centered on each point count location (5 plots 20 m apart on a line in 4 cardinal directions from the center of each point count, or 20 plots/point). Vegetation height (cm) and angle of obstruction (°), measurements of vegetation structure (Harrell and Fuhlendorf 2002), were recorded at one corner of each 0.10 m^2 quadrat.

Statistical Analysis

Effects of fire and grazing management on community structure of vegetation and birds have been analyzed previously (Chapter II), but our goal was to put these effects in a broader, multi-scale context. Thus, we used poisson regression (PROC GENMODE, SAS Institute Inc. 1989) to examine relationships between individual bird species

abundances based on counts and multi-scaled habitat and landscape variables. Poisson regression was chosen since our bird abundance data consisted of counts that closely followed a Poisson distribution. The data set consisted of species level bird abundances and variables from 288 point counts over 3 years. We fitted models for the 10 most common bird species in our study area, summing the bird counts over the 4 sampling periods within each season. Our objective was to investigate differential habitat use based on multi-scaled factors in the grassland bird community, thus only we selected 10 species that were within the grassland bird guild or those known to extensively use grasslands for our analyses (Zimmerman 1993, Zimmerman 1997) (Table 1). Because petroleum structures were found only in the patch treatment, we refitted models using only the patch treatment data for 3 bird species (dickcissel, northern bobwhite, and redwinged blackbird) whose initial model (patch and traditional treatment data) included petroleum structures as a significant variable to confirm that treatment was not a confounding variable. Best fit models were determined by using backward elimination (ie. manually removing variables that had a p-value > 0.15) from each model. All remaining variables in each model had p-values < 0.10. Scaled deviance was used to evaluate the overall fit of the model, with scaled deviance values closer to 1 indicating that the model fit well.

RESULTS

We encountered 30 bird species at 96 point count locations over 3 years. Ten species were sufficiently abundant to construct Poisson regression models. Both treatments contained all landscape variables except petroleum structures, which were found only in the patch treatment (Table 2).

Broad-scale landscape variables

Semi-permanent landscape attributes that were found in both treatments influenced the grassland bird community in terms of habitat use. All broad-scale variables except roads were important for multiple species models (table 3). Presence of pond(s) within 150 m of point count locations positively influenced models for killdeer (*Charadrius vociferous*), common nighthawk (*Chordeiles minor*), redwinged blackbird, and northern bobwhite and did not negatively influence any models. Presence of creek(s) < 150 m of point count locations positively influenced models for killdeer, redwinged blackbird, and mourning dove (*Zenaida aurita*) and negatively influenced models for dickcissel (*Spiza americana*), Henslow's sparrow (*Ammodramus henslowii*), and northern bobwhite. Rock outcrop(s) < 150 m of point count locations positively influenced models for common nighthawk and mourning dove and negatively influenced models for dickcissel, eastern meadowlark (*Sturnella magna*), and redwinged blackbird. Woody edge(s) < 150 m of point count locations positively influenced northern bobwhite and negatively influenced models for grasshopper sparrow (*Ammodramus savannarum*), common nighthawk, and Henslow's sparrow. Petroleum structure(s) < 150 m of point count locations did not positively influence any species models and negatively influenced models for dickcissel, redwinged blackbird, and northern bobwhite. Because petroleum structures were only found in the patch treatment, we refitted models for species with negative associations with petroleum structures using only data from the patch treatment. Petroleum structures remained as a significant negative variable in all 3 models (dickcissel, redwinged blackbird, and northern bobwhite) when analyzed using only patch treatment data. The only significant change in any of these models after we used only the

patch treatment data was the loss of rock outcrop as a significant variable in the dickcissel model.

Fire-Grazing Interaction

All grassland bird species in the analysis were influenced by either treatment or time since focal disturbance (tables 1, 4). Treatment (patch or traditional) was an important variable in 6 of the 10 species models in our analysis. Time since focal disturbance (0, 0.5, 1, 2, and 3 years) was an important variable for 8 of 10 species models. In our species models, patch treatment was coded as 1 (traditional 0); thus, models in which treatment was a positive variable indicated a positive response to our patch treatment by the bird species. Species models that had a positive response to time since focal disturbance indicated a positive relationship with vegetation recovery following disturbance and increased structural density of vegetation (table 1). Bird species whose models had a positive relationship with treatment included upland sandpiper (*Bartramia longicauda*), killdeer, red-winged blackbird, and mourning dove. Bird species whose models had a negative response to treatment included dickcissel and grasshopper sparrow. Species models that indicated a positive response with time since focal disturbance included dickcissel, eastern meadowlark, Henslow's sparrow, and northern bobwhite. Species models that indicated a negative response to time since focal disturbance included upland sandpiper, killdeer, common nighthawk, and mourning dove. Upland sandpiper, killdeer, and mourning dove reached peak abundance in recently burned patches (<1 year since focal disturbance) in the patch treatment (table 1). Grasshopper sparrows reached peak abundance in the traditional treatment and patches with 1-2 years since focal disturbance in the patch treatment (table 1). Eastern

meadowlarks reached peak abundance in patches with 1-2 years since focal disturbance in the patch treatment (table 1). Dickcissels reached peak abundance in the unburned sites in the patch treatment (table 1). Henslow's sparrows were not present in the traditional treatment or recently burned patches (>1 years since focal disturbance) in the patch treatment and increased in abundance with increasing time since focal disturbance in the patch treatment (table 1).

Fine-scale habitat variables

Habitat variables such as vegetation functional groups, bare ground, litter, and vegetation structure that were affected by the fire and grazing interaction were used to create fine-scale models for our 10 grassland bird species (tables 1, 3). All habitat variables influenced some of the species models. Tallgrass cover positively influenced models for dickcissel, common nighthawk, Henslow's sparrow, and northern bobwhite and negatively influenced models for upland sandpiper, killdeer, redwinged blackbird, and mourning dove. Forb cover positively influenced models for dickcissel, Henslow's sparrow, and northern bobwhite and negatively influenced the eastern meadowlark model. Shortgrass cover positively influenced models for common nighthawk and Henslow's sparrow and negatively influenced the upland sandpiper model. Grasslike cover positively influenced models for dickcissel, killdeer, redwinged blackbird, and Henslow's sparrow and did not negatively influence any species models. Bare ground positively influenced models for dickcissel, killdeer, common nighthawk, northern bobwhite, and mourning dove and negatively influenced models for eastern meadowlark, grasshopper sparrow, and upland sandpiper. Litter cover positively influenced models for dickcissel, eastern meadowlark, Henslow's sparrow, and northern bobwhite and

negatively influenced models for upland sandpiper, killdeer, and mourning dove. Shrub cover positively influenced the dickcissel model and negatively influenced models for upland sandpiper, killdeer, redwinged blackbird, and Henslow's sparrow. Vegetation height positively influenced models for common nighthawk, redwinged blackbird, and mourning dove and negatively influenced the grasshopper sparrow model. Angle of obstruction did not positively influence any species models and negatively influenced models for dickcissel, eastern meadowlark, upland sandpiper, common nighthawk, and Henslow's sparrow.

DISCUSSION

Multi-scale factors are important in structuring of grassland bird communities. Bird species within the grassland bird community all had varying relationships to multi-scaled variables in our models, demonstrating the importance of heterogeneity at multiple scales for conservation of grassland biodiversity. Recent work on the influence of heterogeneity on grassland communities indicates that time since disturbance dictates vegetation functional group composition and structure, which drives grassland bird community dynamics (Chapter II). Furthermore, many grassland birds rely on vegetation structural cues for habitat selection (Knopf 1994, Askins 2000). Many landscape features also play an important role in determining grassland bird species assemblages at a broader scale (McGarigal and McComb 1995). Habitat area and patch size have also been identified as important factors in structuring grassland bird communities (Herkert 1994, Helzer and Jelinski 1999); however, our study sites were relatively large unfragemented grasslands (>500 ha) surrounded by a matrix of similarly unfragemented grasslands (>4000 ha); thus, we did not consider habitat area or patch size in our analyses.

Our models did demonstrate that petroleum structures, an anthropogenic landscape variable that has not been considered in past investigations, may influence the local bird community. Presence of petroleum structures was the only anthropogenic landscape variable that had only negative relationships in all models in which it was a significant variable. Our study was not specifically designed to measure the impact of petroleum structures, and because our methods utilized a bird abundance measurement that relied partially on audible identification of species (point counts), our model may not accurately predict the effect of pump jacks on grassland bird species. Nonetheless, further investigation of the impacts of petroleum structures on grassland birds is warranted. Relatively few investigations of the effects of petroleum structures on bird communities have been undertaken, although one recent study noted a reduction in nest initiation of sage grouse (*Centrocercus urophasianus*) < 3 km of natural gas wells in Wyoming, USA (Lyon and Anderson 2003). Wind turbines, which may act similarly to petroleum structures in terms of stature, movement, and noise, were found to lower total grassland bird abundance < 180 m of their presence in CRP fields of southwestern Minnesota (Leddy et al. 1999). It is unclear whether large manmade structures such as petroleum structures and wind turbines act as fragmentation agents in grasslands simply by changing habitat structural cues used by grassland birds, or whether the structures are an actual deterrent to birds due to movement, presence, or noise.

Woody edge has been reported as a fragmentation agent in grasslands, possibly acting as ecological traps for grassland birds by lowering nest success due to increased predation and brood parasitism (Johnson and Temple 1990, Vickery et al. 1994, O'Leary and Nyberg 2000, Winter et al. 2000, Jensen and Finck 2004). Consistent with our

models, past studies have noted that grasshopper sparrows and Henslow's sparrows tend to avoid woody edge habitat (Zimmerman 1988, Delisle and Savidge 1996, Cully and Michaels 2000). Other grassland species, such as dickcissels, may not actively avoid woody edge but may experience lower nesting success near woody edge (Winter et al. 2000). As in our model, northern bobwhite has been positively associated with woody cover (Kopp et al. 1998).

Bird species that use areas near water for feeding, nesting, or other activities (e.g., killdeer, common nighthawk, redwinged blackbird, and mourning dove); (National Geographic Society 1987) had positive associations with landscape features that contained water such as creeks and ponds in our species models. The only landscape feature included in our analyses that did not have any associations with species models was presence of roads. This may be due to the fact that all roads in our study site were unpaved and < 15 m in width, which may not be perceived as fragmentation by grassland birds.

Grazing-fire interaction

Landscape-level heterogeneity provided a means historically for the coexistence of diverse suite of grassland obligate wildlife species with dissimilar habitat preferences; however, the mechanisms associated with heterogeneity may not be currently operating. Prior to European settlement of grasslands of the Great Plains of North America, fire and grazing interacted to create a mosaic of vegetation structure (Knapp et al. 1999, Fuhlendorf and Engle 2001). Intense grazing by bison occurred in recently burned portions of the landscape due to increased forage palatability and access to high quality forage, while unburned areas remained relatively ungrazed. Abundant fuel in unburned

areas led to a higher probability of future fires, while fuel reduction through forage consumption by bison in burned and focally grazed areas led to a lower probability of reoccurring fire, allowing fuel accumulation. Thus, fire altered grazing decisions of herbivores, and grazing influenced the extent and intensity of future fires (Fuhlendorf and Engle 2004). This grazing-fire interaction (grazing-fire model) resulted in a shifting mosaic of vegetation structure across the landscape, with recently burned and grazed areas in a short grazing lawn (McNaughton 1984) with little vertical structure and undisturbed areas consisting of tall, dense vegetation (Steuter 1986, Hobbs et al. 1991, Hamilton 1996, Fulendorf and Engle 2001). Grassland birds evolved within the context of this shifting mosaic, with some species adapted to a fairly narrow range of patch types created under spatially and temporally distinct disturbance regimes. Knowledge of this historical fire-grazing model has led many authors to suggest a management model for grassland birds that emphasizes a shifting mosaic of disturbances on the landscape to increase heterogeneity (Jensen et al. 1999, Askins 2000, Walk and Warner 2000, Fuhlendorf and Engle 2001). Our study demonstrates that shifting focal disturbances can play an important role in conservation of grassland birds by increasing habitat heterogeneity.

Effects of grassland disturbances such as fire, grazing, and haying on grassland birds have been extensively studied (Bock and Webb 1984, Peterson and Best 1987, Jansen et al. 1999, Walk and Warner 2000), but the importance of heterogeneity and interactions among disturbances has not been fully explored. Most studies have noted shifts in bird species composition associated with disturbances, with species preferring relatively dense vegetation decreasing in abundance after a disturbance and species

preferring more open vegetation structure increasing in abundance after a disturbance. In our study, time since focal disturbance was an important variable in the largest number of our species models, apparently driving habitat selection of several grassland bird species. Among fine-scale habitat variables, bare ground, litter cover, and tallgrass cover had the greatest number of species associations in our models. Time since focal disturbance was the primary factor associated with changes in these fine-scale habitat variables. Recent investigations indicate that plant functional group and litter shifts associated with time since focal disturbance strongly influences the composition of the grassland bird community (Chapter II). For instance Henslow's sparrow, a species associated with high amount of litter and herbaceous cover (Cully and Michaels 2000), was absent from patches in the patch treatment with recent focal disturbance (<1 YSFD) and the traditional treatment in which annual fire eliminated litter accumulation. In the patch treatment, Henslow's sparrow abundance increased with increasing time since focal disturbance and associated litter accumulation. In contrast, upland sandpiper, a species associated with more open habitat structure, decreased in abundance with increasing time since focal disturbance. Other species, such as eastern meadowlark, reached peak abundance at intermediate time since focal disturbance. This dramatic difference in habitat use by coexisting grassland bird species demonstrates the importance of disturbance-induced heterogeneity in grassland bird conservation.

Multi-scale management

Successful grassland bird conservation will likely require protection of large (>1000 ha), intact and unfragmented native grasslands (Herkert et al. 2003). We suspect that variability in grassland bird community composition due to fine-scale habitat

variables and disturbance regime is more important in large, intact landscapes than in fragmented landscapes. In fragmented landscapes, grassland area and fragmentation effects such as woody edge and surrounding cultivation may be more important for grassland bird community dynamics than landscape variables and fine-scale habitat variables. Herkert (1994b) found that in grassland fragments, habitat area influenced grassland bird composition more than fire regime. Our site was a large (>1000 ha), intact grassland landscape that contained many landscape variables that are both naturally occurring (rock outcrops, creeks) and anthropogenic (petroleum sites, ponds) within a mosaic of heavily disturbed to relatively undisturbed patches.

At a regional scale, grassland landscapes vary from continuous grasslands to areas highly fragmented by cultivation or invading woody species. These patterns are dependent on topo-edaphic conditions, climate patterns, bio-geographical changes in species distributions, land ownership patterns, regional trends in management, and regional socio-economics. At the spatial scale of remnant, intact habitats, conservation of grassland birds depends on management decisions about, among other things, grazing and fire. We suggest a hierarchical approach to prioritize landscape and habitat factors that influence conservation of grasslands and their associated fauna by classifying each factor in terms of severity of the disturbance and resistance to recovery of those effects. Our approach is based on isolating factors that lead to irreversible changes from factors that lead to changes that are not permanent from a landscape management perspective.

Classification factors according to a framework based on severity of disturbance and resistance to recovery from those effects provide many of the benefits of hierarchy theory because local factors are constrained by those that are associated with broader

spatial scales such as fragmentation. Within grasslands, fragmentation factors that lead to smaller, more isolated fragments of native prairies constrain most of the factors that are associated with local grassland management. This suggests a priority of first reducing fragmentation factors by minimizing factors that lead to conversion of native plant communities that are not reversible in management time frames. In landscapes that are not experiencing any significant effects of fragmentation, conservation efforts should focus on factors that may be associated with local management grasslands.

In contrast, within these large, unfragmented grasslands, management should use relevant ecological processes such as fire and grazing to maintain the range of vegetation heterogeneity that existed within the evolutionary history of grassland ecosystems (Fuhlendorf and Engle 2001). Disturbance thresholds associated with spatio-temporal scale that are critical for grassland bird species should be considered. For example, species-specific area requirements should be considered when patch-level disturbances are planned. To accommodate most grassland bird species-area requirements, disturbance patches may need to be up to 200 ha in size (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999). However, most research on grassland bird species minimum area requirements has been done in fragmented landscapes, thus it is unclear whether minimum area thresholds are applicable to disturbance patches in intact grasslands. Bakker et al. (2002) found that sedge wrens (*Cistothorus platensis*) and clay-colored sparrows (*Spizella pallida*) did not select patches based on size in an unfragmented landscape in mixed and tallgrass prairie. Adequate recovery time after disturbances (>2 years) should be allowed to maintain grassland species, such as Henslow's sparrow, that are intolerant of frequent disturbance. However, disturbances need to be frequent enough

(< 5 years) to maintain grasslands free from woody plant invasion. Thus, decisions concerning grassland bird conservation efforts should maintain a hierarchical approach by considering factors important at multiple spatio-temporal scales.

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Table 1. Abundance of grassland bird species (#/100 m radius point count), percent cover of plant functional groups, and height stratified by treatment (patch or traditional) and time since disturbance (0, 1, 2 years since fire/grazing and unburned) during spring 2001-2003 at the Tallgrass Prairie Preserve, northcentral, Oklahoma.

Variable	Patch				Traditional
	0	1	2	Unburned	1
Dickcissel	2.4	3.5	3.5	4.2	3.2
	(0.3)	(0.1)	(0.2)	(0.6)	(0.1)
Eastern	0.8	1.6	1.5	1.14	1.0
meadowlark	(0.1)	(0.3)	(0.1)	(0.1)	(0.1)
Grasshopper	1.6	1.9	1.8	1.3	1.9
sparrow	(0.2)	(0.1)	(0.1)	(0.1)	(0.1)
Upland	0.75	0.13	0.08	0.06	0.28
Sandpiper	(0.16)	(0.03)	(0.08)	(0.02)	(0.03)
Killdeer	0.34	0.02	0.03	0.05	0.09
	(0.11)	(0.01)	(0.03)	(0.03)	(0.08)
Common	0.15	0.10	0.03	0.09	0.13
nighthawk	(0.03)	(0.04)	(0.03)	(0.3)	(0.02)
Redwinged	0.11	0.32	0.11	0.13	0.10
blackbird	(0.05)	(0.16)	(0.11)	(0.06)	(0.02)
Henslow's	0.0	0.19	0.67	1.1	0.0
sparrow	(0.0)	(0.12)	(0.20)	(0.2)	(0.0)
Northern	0.10	0.15	0.17	0.18	0.15
bobwhite	(0.04)	(0.13)	(0.08)	(0,06)	(0.2)
Mourning dove	0.11	0.03	0.03	0.01	0.04
	(0.06)	(0.02)	(0.03)	(0.01)	(0.01)
Tallgrass (%)	39.3	58.3	69.1	65.5	63.1
	(4.2)	(6.0)	(10.0)	(2.3)	(1.9)
Forb (%)	18.3	20.4	14.9	21.0	18.1
	(4.3)	(2.8)	(0.8)	(7.3)	(2.0)
Bare ground	35.1	7.1	1.1	3.5	20.2
(%)	(2.1)	(2.1)	(0.5)	(0.9)	(1.6)
Litter (%)	2.3	46.1	86.7	88.1	2.1
	(0.4)	(12.9)	(5.7)	(1.7)	(0.8)
Height (cm)	9.6	22.9	32.6	28.2	14.3
	(0.7)	(2.4)	(0.3)	(0.8)	(0.7)

Table 3. Parameter estimates for Poisson regression models in which fine scale habitat variables predict grassland bird species abundance. Data were collected from point count locations (n=288) at the Tallgrass Prairie Preserve, northcentral, Oklahoma during spring 2001-2003. Total model indicates scaled deviance of species model, a goodness of fit test.

Species	Tallgrass	Shortgrass	Grasslike	Forb	Bare ground	Litter	Shrub	Vegetation height	Angle of obstruction	Total model
Dickcissel	0.0064	N/A	0.0074	0.0105	0.0078	0.0012	0.03	N/A	-0.0081	1.08
Eastern meadowlark	N/A	N/A	N/A	-0.0125	-0.0116	0.0027	N/A	N/A	-0.0096	1.21
Grasshopper sparrow	N/A	N/A	N/A	N/A	-0.0144	N/A	N/A	-0.0311	N/A	0.99
Upland sandpiper	-0.0225	-0.0180	N/A	N/A	-0.0337	-0.0234	-0.0639	N/A	-0.0419	1.54
Killdeer	-0.0127	N/A	0.0375	N/A	0.0223	-0.0102	-0.1901	N/A	N/A	1.05
Common nighthawk	0.0159	0.0429	N/A	N/A	0.0478	N/A	N/A	0.0446	-0.0269	1.26
Redwinged blackbird	-0.0129	N/A	0.0171	N/A	N/A	N/A	-0.1198	0.0442	N/A	1.65
Henslow's sparrow	0.0179	0.0396	0.0331	0.0302	N/A	0.0597	-0.1429	N/A	-0.052	0.85
Northern bobwhite	0.0145	N/A	N/A	0.0211	0.0189	0.0065	N/A	N/A	N/A	1.12
Mourning dove	-0.0383	N/A	N/A	N/A	0.0680	-0.0370	N/A	0.218	N/A	0.61

Table 2. Parameter estimates for Poisson regression models in which treatment (patch vs. traditional) and landscape variables predict grassland bird species abundance. Data were collected from point count locations (n=288) at the Tallgrass Prairie Preserve, northcentral, Oklahoma during spring 2001-2003. Total model indicates scaled deviance of species model, a goodness of fit test.

Species	Treatment	Time since dist.	Pond	Creek	Rock outcrop	Woody edge	Petroleum structure	Road	Total model
dickcissel	-0.14	0.15	N/A	-0.07	-0.13	N/A	-0.27	N/A	1.39
eastern meadowlark	N/A	0.08	N/A	N/A	-0.21	N/A	N/A	N/A	1.36
grasshopper sparrow	-0.22	N/A	N/A	N/A	N/A	-0.23	N/A	N/A	1.03
upland sandpiper	0.89	-1.03	N/A	N/A	N/A	N/A	N/A	N/A	1.55
killdeer	1.21	-0.77	0.89	1.07	N/A	N/A	N/A	N/A	1.0
common nighthawk	N/A	-0.16	0.49	N/A	0.58	-0.66	N/A	N/A	1.36
redwinged blackbird	0.70	N/A	0.97	0.58	-1.09	N/A	-0.55	N/A	1.55
henslow's sparrow	N/A	1.32	N/A	-0.29	N/A	-0.35	N/A	N/A	1.13
northern bobwhite	N/A	0.17	0.40	-0.44	N/A	0.39	-1.49	N/A	1.03
mourning dove	1.09	-0.83	N/A	1.16	1.24	N/A	N/A	N/A	0.71

CHAPTER IV

INFLUENCE OF DISTURBANCE INDUCED HETEROGENITY ON PLANT COMPOSITION AND DIVERSITY IN TALLGRASS PRAIRIE

ABSTRACT

Heterogeneity has been identified as critical in the maintenance of many ecosystems and can be considered a foundation of ecosystem management. We propose that management models of grasslands that use disturbances such as grazing and fire to simulate the range of heterogeneity within the context of grassland evolution can maintain and enhance biological diversity. We compared a homogeneity-based management model (traditional treatment) to a management model in which heterogeneity was based on evolutionary grazing and fire interactions (patch treatment) to evaluate the role of disturbance induced heterogeneity in structuring plant species diversity. Vegetation composition in a tallgrass prairie was estimated by cover of species in the late growing season (July and August) of 2001 to 2003. Most differences in plant species, total plant cover, functional group cover, richness, and diversity occurred at the patch level in the patch treatment and were dictated by time since focal disturbance. Heterogeneity of total plant cover, *Schizachyrium scoparium* cover, forb cover, litter, and bare ground in the patch treatment was greater than in the traditional treatment. Results from this experiment indicated that patch applications of fire and subsequent grazing in tallgrass prairie can alter late-season plant community dynamics compared with uniform applications of fire and grazing; however, effects were generally short-lived (< 3 years).

Differences in the spatial and temporal application of disturbance (fire followed by grazing) appeared to be the driving force in plant diversity rather than fire and grazing per se. Plant species composition did not exhibit any permanent shifts associated with intense selective grazing in our patch treatment. Our data and other recent studies suggest that homogenous management models can lead to declining biodiversity.

Keywords: disturbance, fire, grazing, heterogeneity, intermediate disturbance hypothesis, species diversity, tallgrass prairie

INTRODUCTION

Maintaining plant diversity within the range of historical background levels has become a conservation priority (Howe 1994, Olff and Ritchie 1998, Bestelmeyer et al. 2003). This has led to numerous investigations of mechanisms involved in maintaining species diversity including competition, resource availability, dispersal, resource heterogeneity, and natural disturbance (Armesto and Pickett 1985, Huston 1994, Bakker et al. 2003, Bestelmeyer 2003, Harrison et al. 2003). Among these mechanisms, heterogeneity has been identified as critical in the maintenance of many ecosystems and is often considered a foundation of ecosystem management (Christensen 1997, Ostfeld et al. 1997, Fuhlendorf and Engle 2001). Geomorphologic features combined with variability in resources can contribute to resource heterogeneity (Burnett et al. 1998, Fuhlendorf and Engle 2004). Natural disturbance processes can alter resources availability, but typically these processes are evaluated in terms of relatively homogeneous spatial patterns. Disturbance often is not uniform and may actually lead to complex biotic interactions that can contribute to a shifting mosaic of patch-level

heterogeneity across the landscape (Knapp et al. 1999, Bakker et al. 2003, Fuhlendorf and Engle 2004). Increases in species diversity associated with a shifting mosaic are most frequent in ecosystems with relatively high productivity, such as mesic grasslands.

In the Great Plains grasslands of North America, fire at multiple spatial and temporal scales followed by grazing of large herbivores acted as primary agents of disturbance-induced heterogeneity through their interactive contribution to a shifting mosaic (Vinton et al. 1993, Hartnett et al. 1996, Fuhlendorf and Engle 2001). Disturbance-induced heterogeneity played a key role in the evolution and maintenance of biodiversity in Great Plains grasslands by the creation of a gradient of patch types in multiple stages of structural and compositional plant succession with some patches existing as a grazing lawn (McNaughton 1984) created through recent fire and intense herbivore selection, others in a transitional recovery stage, and still others consisting of a dense, comparatively undisturbed vegetation in a high seral stage (Steuter 1986, Hobbs et al. 1991, Hamilton 1996, Fuhlendorf and Engle 2001). This variability in disturbance gradients allowed for the existence of relatively rare forb species that require open space for recruitment and establishment while maintaining areas of high biomass dominated by matrix forming perennial grass species within the context of a relatively productive ecosystem. Thus, transient, disturbance induced heterogeneity allowed for the coexistence of a diverse floral and faunal community with differing life history requirements.

Europeans have perceived North American presettlement tallgrass prairie landscapes as a homogenous landscape dominated by late successional perennial grasses (Howe 1994). Recent evidence concerning animal behavior and presettlement fire

regimes rejects the notion of a static, homogenous tallgrass prairie landscape (Howe 1994, Fuhlendorf and Engle 2001). Nonetheless, the presettlement view of grasslands has probably contributed to the current management model of grasslands in which uniform, moderate disturbances are applied in an attempt to maximize production and minimize resource degradation (Holechek et al. 2003). This management model maximizes dominance by a few large, perennial grass species. Agriculturalists have attempted to improve the distribution of grazing animals through the use of specialized grazing systems and increasing water sources to decrease spatial heterogeneity under the assumption of increased livestock production and reduced ecosystem degradation (Fuls 1992, Bailey et al. 1998, Fuhlendorf and Engle 2001, Holechek et al. 2003).

In contrast, conservationists, working under a different set of objectives than agriculturalists, have frequently used dormant-season fire and exclusion of grazing to promote dominance by warm season perennial grasses under the pretext of maintaining the presettlement view of a grass dominated prairie. We propose that management models of grasslands that use disturbances such as grazing and fire to simulate the historical range of heterogeneity within the context of grassland evolution can maintain and enhance biological diversity. We compared a traditional homogeneity-based management model to a management model in which heterogeneity is based on evolutionary grazing and fire interactions (Fuhlendorf and Engle 2001) to evaluate the role of disturbance induced heterogeneity in structuring biodiversity. Specifically, our objective was to evaluate the effect of time since focal disturbance and treatment on vegetation composition and diversity.

METHODS

Site description

Our study took place on the Tallgrass Prairie Preserve (TGPP) in northcentral Oklahoma, USA (36° 50′N, 96° 25′W), owned and operated by The Nature Conservancy, during 2001 to 2003. The Preserve lies within the southern portion of the Flint Hills region of the Great Plains and contains one of the last remaining examples of large, uncultivated tallgrass prairie habitats in North America. The climate is temperate, with hot summers (average high of 33.9 C for July 2001 to 2003) and cold winters (average low of -4.8 C for January 2001 to 2003). Growing-season (April to October) precipitation for the area was 341mm, 661mm, and 821mm for 2001, 2002, and 2003, respectively. Long-term average (1971 to 2000) growing precipitation (April to October) for the area was 719 mm. Dominant grass species include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Nash), Indian grass (*Sorghastrum nutans* Nash), tall dropseed (*Sporobolus compositus*), and switchgrass (*Panicum virgatum* L.). Dominant forb species include western ragweed (*Ambrosia psilostachya*), ironweed (*Vernonia baldwinii*), and heath aster (*Aster ericoides*). Dominant woody species include *Rubus oklahomus* and *Sumac spp.*

Experimental design

We chose 4 management units within the TGPP that varied in size from 400 to 900 ha. We randomly selected management units (n = 2) which were divided into 6 approximately equal area patches as patch treatments (Fuhlendorf and Engle 2004). These management units had exterior fences, but no dividing fences between the patches. We conducted prescribed burns in the spring (March) and autumn (August to December)

on discrete patches within the patch treatment management units (average patch size 100 ha) annually (2001-2003) (Table 1, Figure 1), resulting in a 3-year fire return interval for each patch in the patch treatment. Recently burned patches received heavy use by cattle, thus creating patches with focal disturbances within the patch treatment. Patches that had not been recently burned were not heavily used by cattle, allowing recovery of vegetation. This shifting of focal disturbance resulted in a mosaic of recently burned patches, recovering patches, and unburned patches that we lumped into categories according to time since focal disturbance in the patch treatment (Table 1). Unburned patches were those patches in the patch treatment that had not been burned during the study at the time of sampling (Table 1). The remaining management units were designated as controls or our "traditional treatment" (n = 2) in which we conducted annual spring (March) burns uniformly across the management units (Table 1).

The traditional treatment, used over the vast majority of the Flint Hills region (Robbins and Ortega-Huerta 2002), consists of annual, complete spring burns accompanied with the introduction of livestock from mid-April to mid-July. Even though we uniformly burned the control management units, we arbitrarily divided each unit into 6 patches and designated as "all burn patches" to compare the traditional treatment to the patch treatment at a patch level. A single exterior fence enclosed each management unit in both treatments. Cattle were introduced in patch treatment and traditional treatment management units from about 15 April to 20 July at a rate of 1.2 ha/animal. Cattle had free access to all patches within each management unit, so cattle could choose between burned and unburned patches in the patch treatment. Cattle chose to graze burned areas in the patch treatment, thus stocking density (number of cattle/grazed area) on burned

patches in the patch treatment was roughly 3 times the stocking density in the traditional treatment.

Vegetation methods

Vegetation composition was estimated by species in the late growing season (late July-early August) of 2001-2003. Cattle have been removed from management units for > 2 weeks prior to vegetation sampling. Each management unit (n = 4) contained 6 patches, and each patch contained 4 vegetation sampling points, for a total of 24 sampling points per management unit (Figure 1). We sampled vegetation composition by canopy cover in 0.10 m^2 quadrats (20 X 50 cm) from 4 sampling points in each patch (24 sampling points per management unit). We estimated vegetation composition in quadrats placed along lines in 4 cardinal directions from the center of each sampling point, with each quadrat 20 m apart (16 quadrats per sampling point) (Figure 1). (Daubenmire 1959). Litter cover and bare ground were also estimated in each quadrat. Nomenclature for plant species follows Diggs et al. 1999.

Statistical Analysis

Species-level vegetation composition at the patch-level was subjected to an indirect gradient analysis (Detrended Correspondence Analysis-DCA) using default options with PCORD software (Jongman et al. 1987, Fuhlendorf and Engle 2004) as a multivariate approach. DCA has been used to summarize general similarities and differences among vegetation communities and can quantify compositional dynamics over time (Collins 2000). We averaged sampling point data within patches (4 point counts per patch) to analyze patch level differences and within management units (6 patches per management unit) to analyze management level differences. This allowed us

to evaluate the effect of time since focal disturbance and treatments on vegetation composition. Initial analyses were based on all species, downweighting rare species in the DCA. We then lumped species into 8 functional groups to look for general trends in the vegetation in response to grazing and fire treatments. Functional groups consisted of tallgrasses (*Andropogon gerardii*, *Tripsacum dactyloides*, *Sorghastrum nutans*, *Tridens flavus*, *Panicum virgatum*, and *Sporobolus compositus*), other perennial grasses (20 species), annual grasses (*Bromus spp., Hordeum pussillum, and Vulpia octoflora*), grasslikes (2 genuses, 1 species), forbs (54 species), legumes (12 species), and woody plants (5 species) (Fuhlendorf and Engle 2004). We kept *Schizachyrium scoparium* separate from other grasses because of its unique growth form, dominance and perceived sensitivity to fire and grazing. We also analyzed several individual forb species that were particularly dominant or of local interest. We then computed means and standard errors for DCA axis scores, individual plant species, functional groups, bare ground, and litter at the treatment and patch level. Species richness, diversity (H'), and eveness were calculated at the treatment and patch level. Differences among treatments and patches were classified as significant if standard errors did not overlap. We used the mean of the standard deviation among patches within a management unit for total plant cover, forb cover, *Schizachyrium scoparium*, bare ground, and litter cover to assess patch-level heterogeneity.

RESULTS

Detrended Correspondence Analysis

We identified 104 plant species. Detrended Correspondence Analysis of patch level species composition data resulted in axis 1 and 2 eigenvalues of 0.186 and 0.117,

respectively. On DCA axis 1, the plant species with the greatest influence based on the DCA species loading scores included *Digitaria ischaemum*, *Froelichia spp.*, *Ulmus americana*, *Gaura coccinea*, and *Lespedeza capita*. For DCA axis 2, the plant species with the greatest influence based on the DCA species loading scores included *Hordeum pusillum*, *Echinochloa crus-galli*, and *Helenium amarum* var. *amarum*. None of the species that were influential on DCA axis 1 or 2 constituted > 1% average plant cover in our treatments, with many being restricted to a specific site. The DCA did not exhibit a strong relationship between plant community dynamics and our treatments or time since focal disturbance (Figures 1, 2), thus we applied univariate methods to further investigate relationships between dominant plant species and functional groups and our treatments and time since focal disturbance (Figure 1).

Traditional and Patch treatment and time since focal disturbance

At the management unit level, most plant species, functional groups, richness, and diversity were not different between the traditional and patch treatments (Figure 2). Forb cover was greater in the patch treatment than the traditional treatment in 2001 and 2003. Tallgrass cover and *Schizacharium scoparium* cover differed among years but not between treatments (Figure 2). Most differences in plant species cover, total plant cover, functional group cover, richness, and diversity occurred for patches within the patch burn treatment and the traditional treatments and were dictated by either time since focal disturbance or season of fire. Several abundant plant species, functional groups, total plant cover, and diversity were influenced by time since focal disturbance (Figure 1). Diversity (H') increased following recent focal disturbance (0-24 months since focal disturbance) in the patch treatment, but declined below pre-burn levels (>36 months since

focal disturbance) by 25-36 months since focal disturbance. Diversity in the traditional treatment was similar to the patch treatment throughout the study (Figure 2). Plant species richness did not change significantly in response to time since focal disturbance or treatment. Total plant cover initially decreased after focal disturbance in the patch treatment but increased to levels greater than pre-burn patches (>36 months) by 25-36 months since focal disturbance. Total plant cover in the traditional treatment was lower than all patches in the patch treatment except 0-12 months since focal disturbance patches. All patches within the traditional treatment had < 1% litter cover due to annual spring fires which eliminated most litter, whereas litter in the patch treatment was dictated by time since focal disturbance (Figure 1). The most recently disturbed (0-13 months since focal disturbance) patches in the patch treatment had minimal litter cover, while the recovering patches (13-36 months since focal disturbance) had high litter cover, exceeding pre-burn (>36 months) patches (Figure 1). Bare ground was highest following recent focal disturbance (0-13 months since focal disturbance) but decreased to less than pre-burn levels (>36 months) by 25-36 months since focal disturbance in the patch treatment. The traditional treatment had less bare ground than patches with recent focal disturbance (0-13 months since focal disturbance) but more bare ground than the rest of the patches in the patch treatment. Tallgrass cover exhibited a slight increase with time since focal disturbance in the patch treatment. *Schizachyrium scoparium* cover, the dominant grass species in our study area, decreased following recent focal disturbance (0-13 months since focal disturbance) in the patch treatment but increased to levels greater to the traditional treatment and pre-burn patches (>36 months) in the patch treatment by 24-36 months since focal disturbance. Forb cover increased following recent focal

disturbance (0-13 months since focal disturbance) but declined to pre-burn (>36 months) by 25-36 months since focal disturbance in the patch treatment. Forb cover was greater in recently burned patches (0-13 months since focal disturbance) in the patch treatment than in the traditional treatment or patches within the patch treatment with >24 months since focal disturbance. *Ambrosia psilostachya*, the dominant perennial forb in our study area, initially increased after focal disturbance (1-12 months since focal disturbance and 13-24 months since focal disturbance) in the patch treatment, but decreased to levels similar to the pre-burn levels in the patch treatment (>36 months) and the traditional treatment by 25-36 months since focal disturbance. Annual grasses decreased following focal disturbance in the patch treatment and did not recover to preburn (>36 months) levels during the study.

Season of fire in our patch treatment only affected a few forb species such as *Ambrosia psilostachya* and *Gutierrezia dracunculoides*. *Ambrosia psilostachya* maintained higher levels in spring burn patches than in fall burn patches for 0-24 months since focal disturbance in the patch treatment (Figure 1). *Gutierrezia dracunculoides*, an annual forb, had slightly, but not significantly higher levels (2%) in the autumn burns (0-24 months since focal disturbance) compared to spring burns (0-24 months since focal disturbance) in the patch treatment (data not shown). Season of fire did not significantly affect any grass species or overall cover or diversity.

Heterogeneity (indexed by standard deviation among patches) of total plant cover, S*chizachyrium scoparium* cover, and forb cover in the patch treatment was greater than the traditional treatment in 2001 and 2003 (Figure 3). Heterogeneity in litter among patches was as much as 40 times greater in the patch treatment than the traditional

treatment during the study (Figure 3). Heterogeneity of bare ground decreased in both treatments across the 3 years of the study but remained higher in the patch treatment during the study (Figure 3).

DISCUSSION

Results from this experiment indicated that patch applications of fire and subsequent grazing in tallgrass prairie can alter late season plant community dynamics compared with uniform applications of fire and grazing, but the effects generally last > 3 years and usually occur at a patch level within management units rather than between management units. Heterogeneity of vegetation composition was greater in the patch treatment than the traditional treatment at the management unit level. Our DCA did not show clear relationships with treatment or time since focal disturbance, indicating that year to year variability, site variability, and random variability interacted to influence late season species composition based on individual species. Our treatments had a strong effect on composition and diversity of individual plant species and functional groups by creating a gradient of disturbance in the patch treatment that included sites recently and intensively disturbed and sites that have not been disturbed for several years. Recent investigations of early season functional group composition and vegetation structure in relation to patch treatments demonstrated stronger relationships with time since focal disturbance than our investigation of late season plant community change (Fuhlendorf and Engle 2004, Chapter II), indicating that vegetation structure may be more responsive to spatially distinct applications of disturbance and time since focal disturbance than species composition. Heterogeneity, either disturbance-induced or geomorphologic, often plays a role in the maintenance of productivity and biodiversity in many ecosystems

(Collins 1992, Burnett et al. 1998, Adler et al. 2001, Fuhlendorf and Engle 2001, Benton et al. 2003). Alterations in spatial heterogeneity can affect habitat diversity, potentially influencing multiple groups of species within an ecosystem (Wiens 1974, Adler et al. 2001).

Disturbance patterns and processes

Fire and grazing have long been identified as essential disturbances in the maintenance of grasslands (Collins 2000, Fuhlendorf and Engle 2001, Harrison et al. 2003). In tallgrass prairie, fire and grazing maintain grassland structure and productivity through removal of litter and woody vegetation and altering plant competitive interactions (Kucera and Koelling 1964, Collins 1987). Generally, disturbances applied for grassland management have been applied uniformly on the landscape to minimize spatial variability (Fuhlendorf and Engle 2001). In addition, most investigations of fire and grazing effects in grasslands have focused on spatially uniform applications of disturbance and their individual effects rather than their interactive effects in the context of a shifting mosaic as our study attempted (Engle and Bidwell 2001). However, evidence concerning the evolutionary history of grassland disturbances suggests that fire and grazing rarely occurred as independent events, but as interactive forces. In the Great Plains of North America, intense bison (*Bos bison*) grazing often occurring in recently burned areas, creating patches with reduced fuel loads (Fuhlendorf and Engle 2004). Patches with reduced fuel loads were unlikely to burn again until bison moved to a more recently burned patch, allowing fuel accumulation in the original burned patch (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001).

Current land management in tallgrass prairie involves use of prescribed fire applied uniformly to a management unit in the late dormant season as in our traditional treatment. Late dormant season fires in tallgrass prairie generally increase matrix-forming, highly palatable perennial grasses and decrease annual grasses and forbs, often lowering plant species diversity (Abrams et al. 1986, Collins 1987). Conversely, grazing in tallgrass prairie decreases highly palatable perennial grasses and increases abundance of annual grasses and forbs, which can increase species diversity by creating open areas for plant establishment (Collins 1987). Frequently, grazing follows use of late dormant season fire in tallgrass prairie, which can increase plant diversity more than grazing alone (Collins 1987). Thus, the interaction of fire and grazing appears to be more important in the structuring of grassland ecosystems than the individual effects of these disturbances. However, other studies have viewed the grazing-fire interaction as a statistical feature where both occur simultaneously. Our reference to interactive effects refers to the attempt to mimic the shifting mosaic that was important in presettlement grasslands.

In our study, spatial and temporal patterns of disturbance were the most important factors in determining effects of disturbance on grassland ecosystem structure. Both of our treatments included fire and grazing, however the differences in the spatial application of fire combined with subsequent herbivore selection for recently burned patches in the patch treatment produced differences in plant community structure across time since focal disturbance gradients that were not apparent at the treatment level. Recently burned patches (0-13 months since focal disturbance) in the patch treatment had higher plant diversity than other patches with varying time since focal disturbance in the patch treatment or the traditional treatment. The recently burned patches (0-13 months

since focal disturbance) had the lowest total plant cover, lowest tallgrass cover, lowest *Schizachyrium scoparium* cover, lowest litter cover, greatest forb cover, and greatest amount of bare ground. Plant diversity declined with increasing time since focal disturbance in the patch treatment as total plant cover and perennial grasses increased, reaching a minimum by 25-36 months since focal disturbance. This data supports past investigations of diversity relationships in mesic prairie that suggest diversity is maximized when matrix-forming perennial grasses and total plant cover are reduced, creating open areas available for recruitment and establishment by forbs and other subdominant species (Abrams et al. 1986, Collins 1987, Hobbs and Huenneke 1992, Copeland et al. 2002). Perhaps a more important conclusion from our study is that differences in the spatial and temporal application of disturbance can be the driving force in plant diversity rather than fire and grazing per se.

Biological diversity

Biological diversity has been discussed traditionally under the pretext of species richness; however, variability in vegetation structure, functional groups, community structure, and landscape pattern at multiple scales also can be used to describe biodiversity (West 1993). Our discussion of biological diversity in this study is focused on patterns of species diversity; however, we acknowledge that other measurements of diversity are useful in describing ecosystem structure and function. Biological diversity from a species richness standpoint is often highest under disturbance regimes that closely resemble type, intensity, frequency, and pattern of disturbances under which the ecosystem developed (Hobbs and Huenneke 1992, Fuhlendorf and Engle 2001). In mesic prairies, the historical disturbance regime consisted of spatially and temporally variable

fire followed by intense herbivore selection as described in the fire-grazing model (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001). Our study attempted to mimic the historical interaction of fire and grazing in tallgrass prairie and investigate patterns of diversity and plant community dynamics. We found that spatial pattern of disturbance may be as important in describing patterns in species diversity as disturbance intensity or frequency.

The intermediate disturbance hypothesis (IDH) has often been used as a means to describe the relationship between disturbance and diversity, predicting an initial increase in diversity with the introduction of disturbance due to changes in competitive interactions, followed by an eventual decline in diversity as disturbance intensity increases (Connell 1978, Huston 1994). Some authors have questioned whether "intermediate" best describes the intensity of disturbance when it occurs, the amount of area affected by disturbance, or the frequency of disturbance (Petraitis et al. 1989, Collins et al. 1995). Studies from the tallgrass prairie have questioned whether the IDH best describes patterns occurring within a disturbance patch, or patterns at a broader scale, encompassing disturbed and undisturbed patches on the landscape similar to our patch treatment (Collins 1992, Collins et al. 1995).

In our study, the patch treatment had high disturbance intensity in the recently burned patches (ie. patches burned followed by intense grazing) and intermediate disturbance frequency and size (3 year fire return interval on individual patches within a unit). This resulted in the patch treatment having the most diverse patch type (0-13 months since focal disturbance) as well as the greatest heterogeneity in litter, bare ground, total plant cover, forb cover, and *Schizachyrium scoparium* cover among patches

within a management unit or between treatments. Greater heterogeneity in the patch treatment can be attributed to variable time since focal disturbance among patches, resulting in increased patch level differences. This suggests that spatial and temporal variability of disturbance in relation to the evolutionary history of an ecosystem are as important in describing diversity relationships as intermediate disturbance in terms of intensity, frequency, or extent. Spatially discreet disturbance patches on the landscape in varying stages of recovery may produce greater landscape-level diversity than spatially uniform disturbances at given intensities or frequencies, as has often been described in the literature.

Management Implications

Fire and grazing generally have been considered as independent disturbances in grasslands; however, evolutionary history of Great Plains grasslands suggests that the interaction of these disturbances on ecosystem at multiple spatial and temporal scales was critical in structuring plant and animal communities. Specifically, fire followed by intense herbivore grazing at multiple scales on the landscape can interact to create a shifting mosaic of vegetation patches in various stages of recovery as described in the fire-grazing model (Fuhlendorf and Engle 2001). This disturbance regime can create a gradient from patches with lower total plant cover that increase recruitment and establishment of forb species, increasing species diversity, to relatively undisturbed patches dominated by perennial grass cover. At the landscape level, multiple patch types exist, contributing to diversity at multiple trophic levels.

Management recommendations in the past have suggested that heavy, selective patch grazing and late growing-season fire may lead to resource degradation including

lowered seral stage (Wright 1974, Fuls 1992). Our data indicate that tallgrass prairie is resilient to intense levels of disturbance (in relation to fire and grazing), with cover of dominant perennial grass species, forb cover, and litter cover returning to pre-disturbance levels within 2-3 years. Plant species composition did not exhibit any permanent shifts associated with intense, selective grazing in our patch treatment, presumably because cattle generally grazed new patches soon after they were burned, allowing less recently burned patches to recover. Time since focal disturbance, not season of fire, was the primary driver of compositional shifts in our study. Season of fire on our study site did not lead to any significant compositional changes.

Uniform applications of fire and grazing typically have been used in grassland management to increase grazing efficiency, under the assumption that homogenous landscapes facilitate increased livestock production while reducing long-term resource degradation associated with static patch-level disturbances (Holechek et al. 2003, Fuhls 1992). Our data and other recent studies suggest that homogenous management models can lead to declines in biodiversity (Fuhlendorf and Engle 2001, Chapter II).Dormant season fires applied annually in the tallgrass prairie region have led to reductions in rare plant species (Kucera and Koelling 1964, Collins 1987) and native prairie biota such as grassland bird species that require heterogeneous, patchy environments (Robbins and Ortega-Huerta 2002, Chapter II).

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Table 1. Burn schedule for patch and traditional treatments at the Tallgrass Prairie Preserve, northcentral OK. M indicates months since patch was burned.

	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5	Patch 6
Patch						
2001	Burned	Burned	Unburned	Unburned	Unburned	Unburned
2002	13-24 M	13-24 M	Burned	Burned	Unburned	Unburned
2003	25-36 M	25-36 M	13-24 M	13-24 M	Burned	Burned
Traditional						
2001	Burned	Burned	Burned	Burned	Burned	Burned
2002	Burned	Burned	Burned	Burned	Burned	Burned
2003	Burned	Burned	Burned	Burned	Burned	Burned

Figure 1. DCA axis 1 and 2 scores, plant species richness and diversity, canopy cover of selected plant species and functional groups in patch treatment stratified by season, months since last focal disturbance (patch treatment) and traditional treatment.

Figure 1.

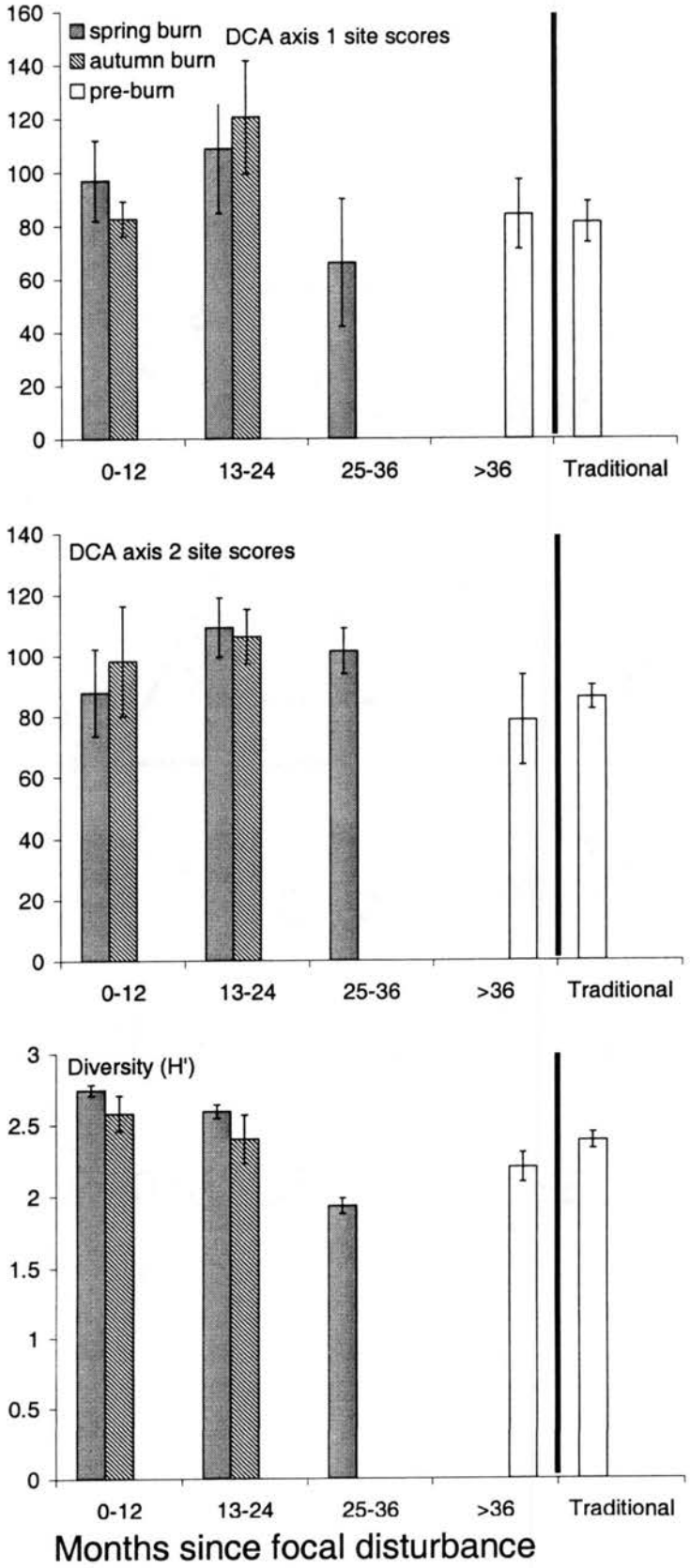

spring burn
autumn burn
pre-burn
DCA axis 1 site scores
160
140
120
100
80
60
40
20
0
0-12
13-24
25-36
>36
Traditional
DCA axis 2 site scores
140
120
100
80
60
40
20
0
0-12
13-24
25-36
>36
Traditional
Diversity (H')
3
2.5
2
1.5
1
0.5
0
0-12
13-24
25-36
>36
Traditional
Months since focal disturbance

Figure 1 continued.

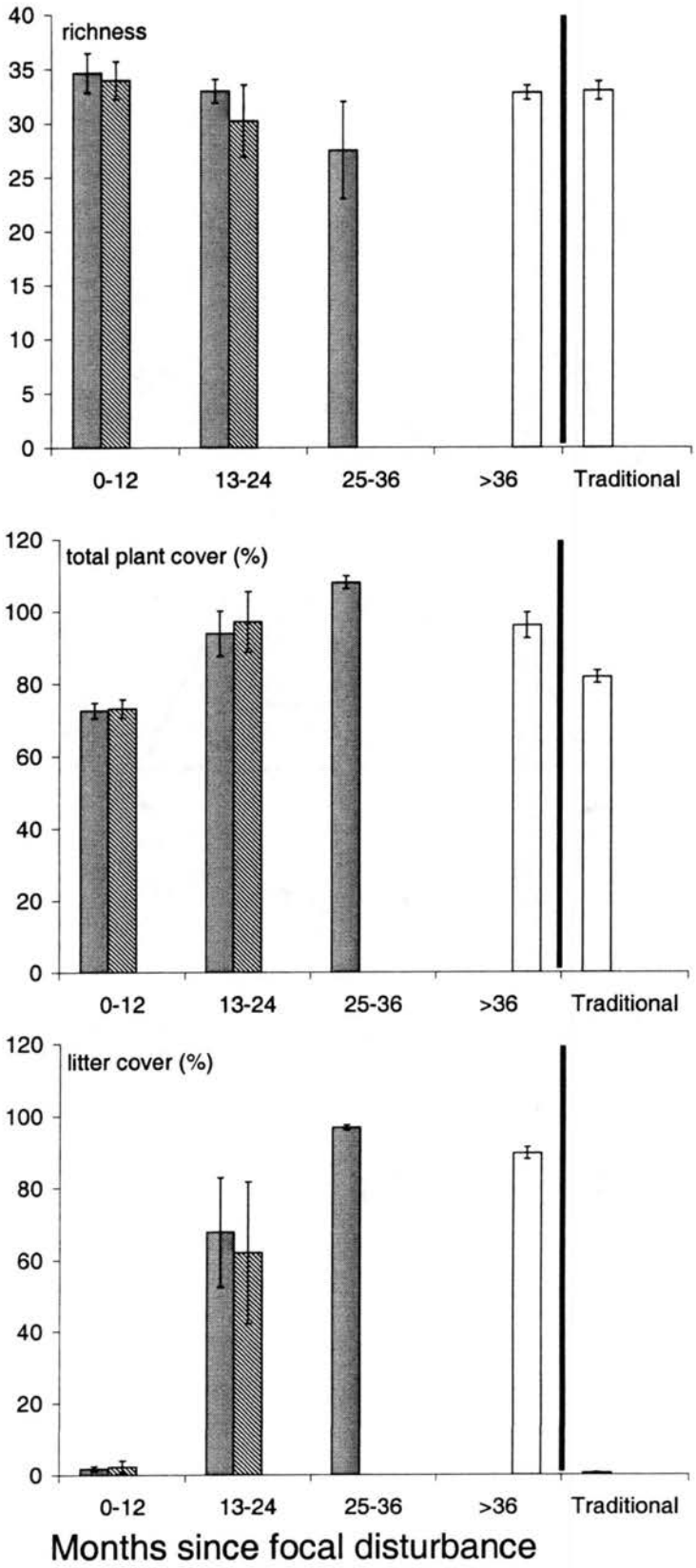


Figure 1 continued.

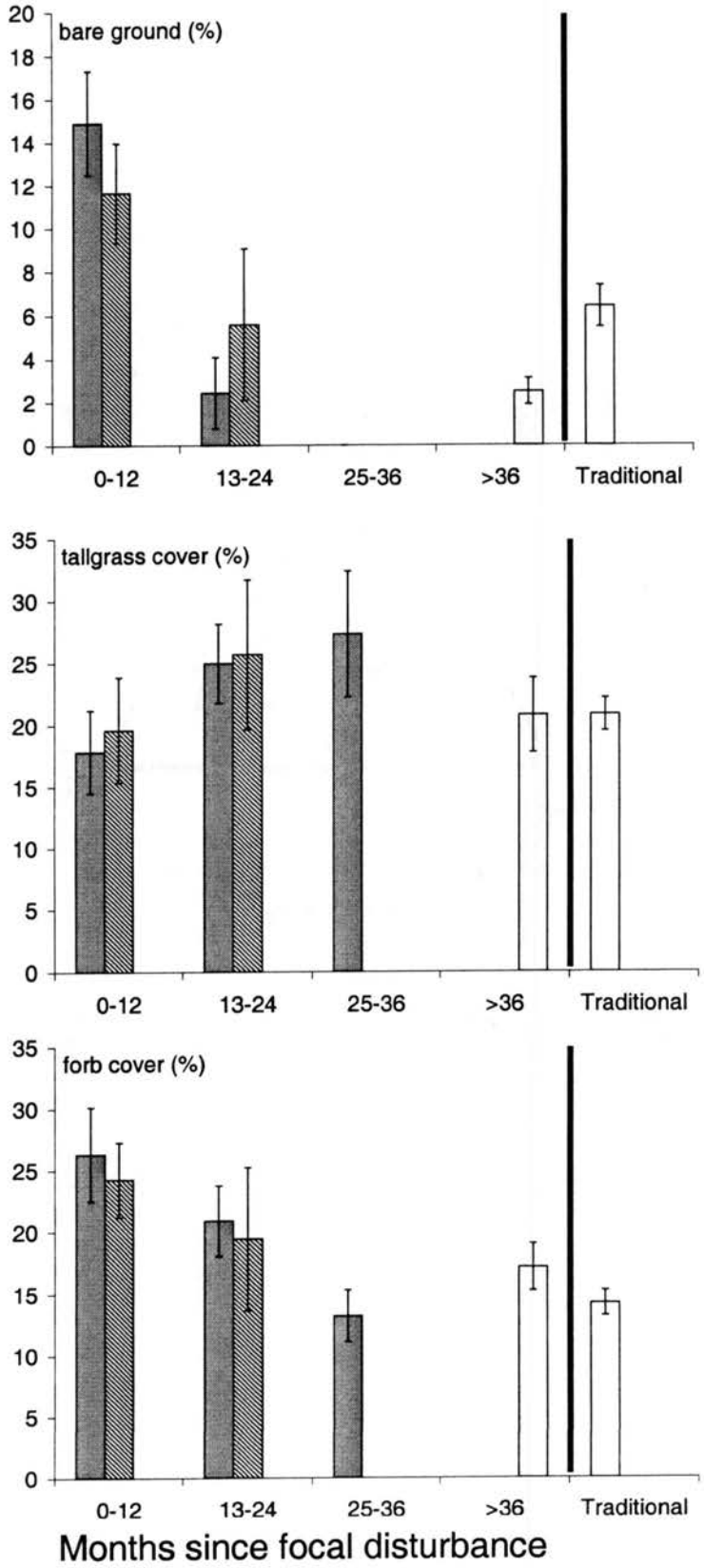


Figure 1 continued.

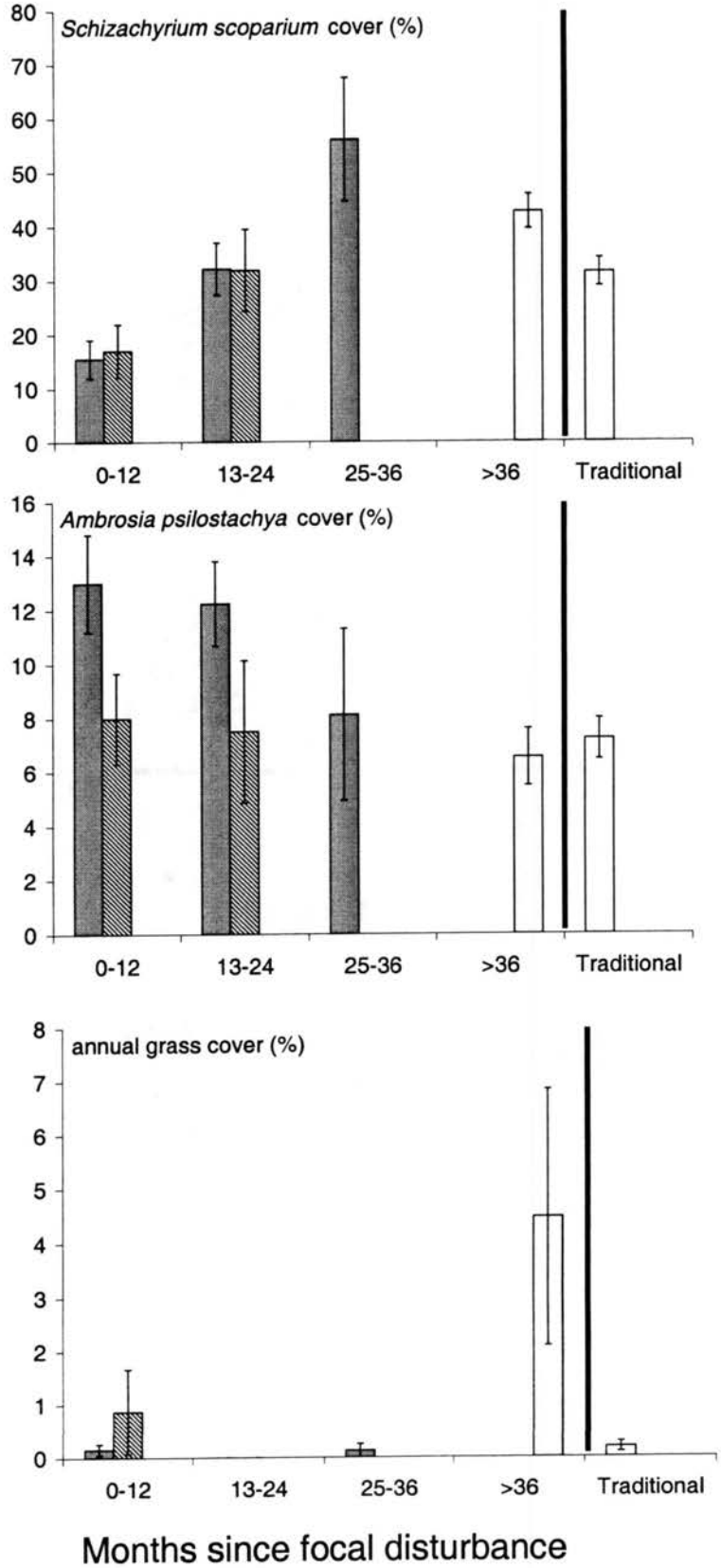


Figure 2. DCA axis 1 scores, plant species diversity, canopy cover of selected plant species and functional groups in patch treatment stratified by year and treatment.

Figure 2.

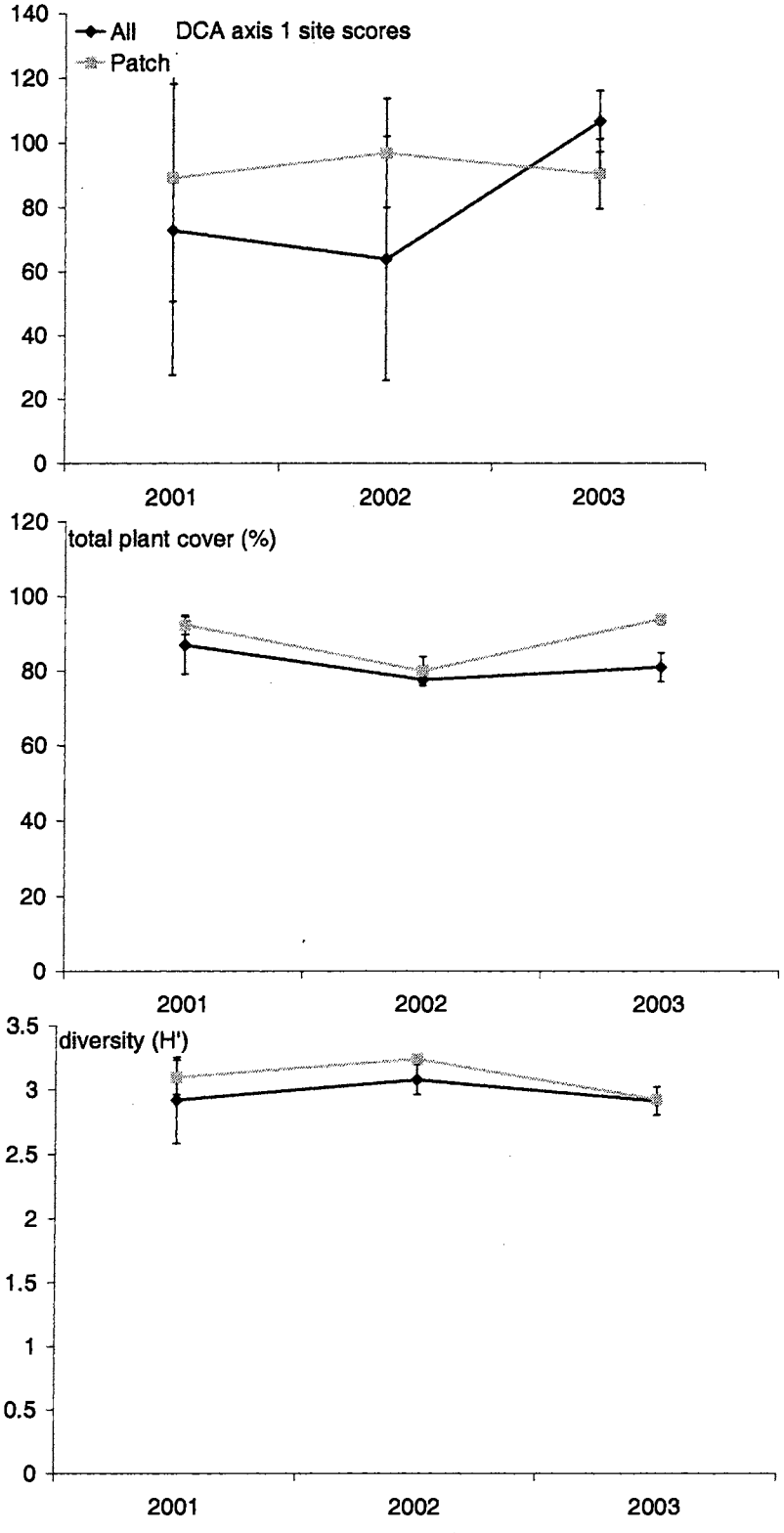

All
Patch
DCA axis 1 site scores
140
120
100
80
60
40
20
0
2001
2002
2003
total plant cover (%)
120
100
80
60
40
20
0
2001
2002
2003
diversity (H')
3.5
3
2.5
2
1.5
1
0.5
0
2001
2002
2003
Year

Figure 2 continued.

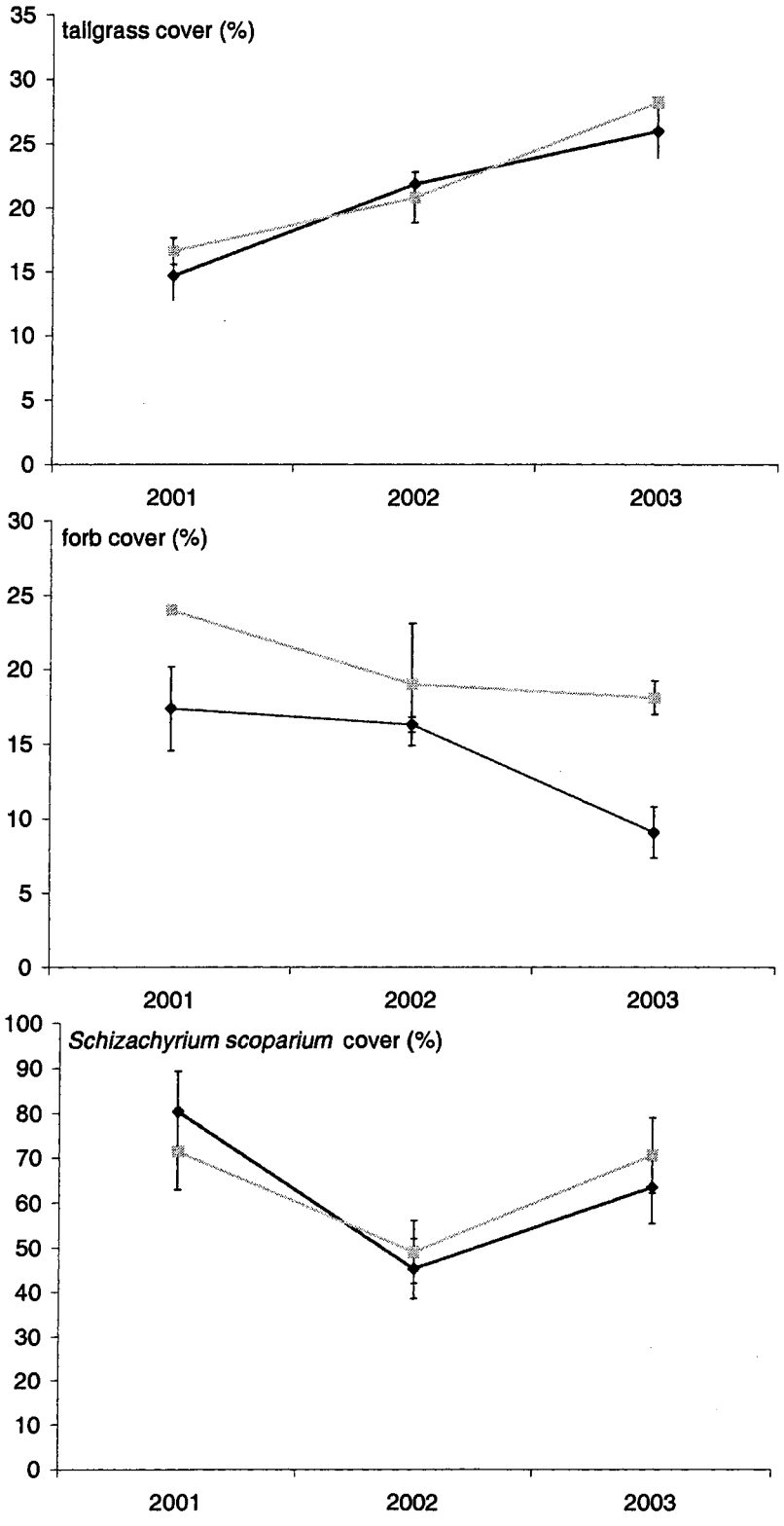


Figure 3. Heterogeneity of total plant cover, selected functional groups, bare ground and litter cover stratified by year and treatment. Heterogeneity is measured as the standard deviation among patches within a single management unit.

Figure 3.

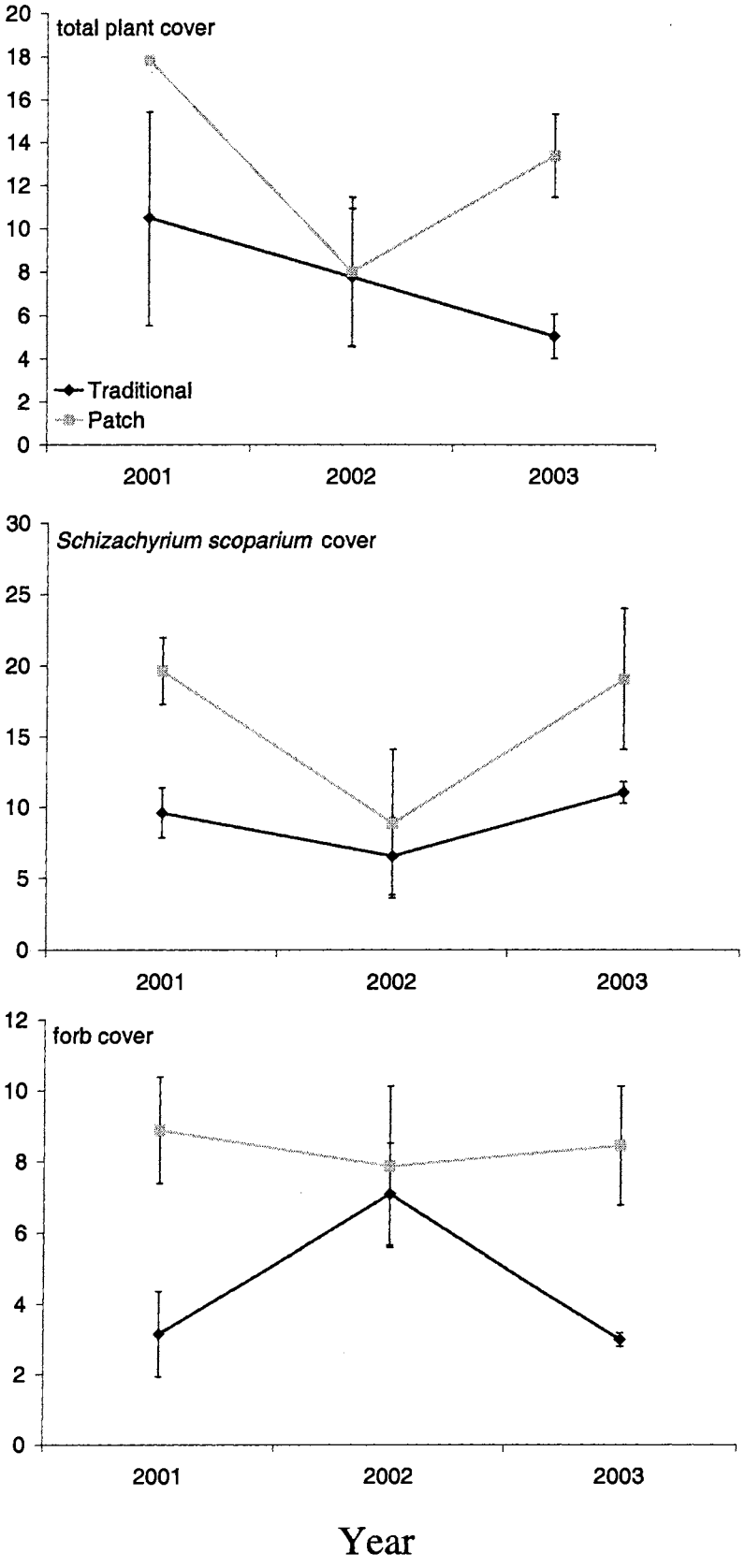
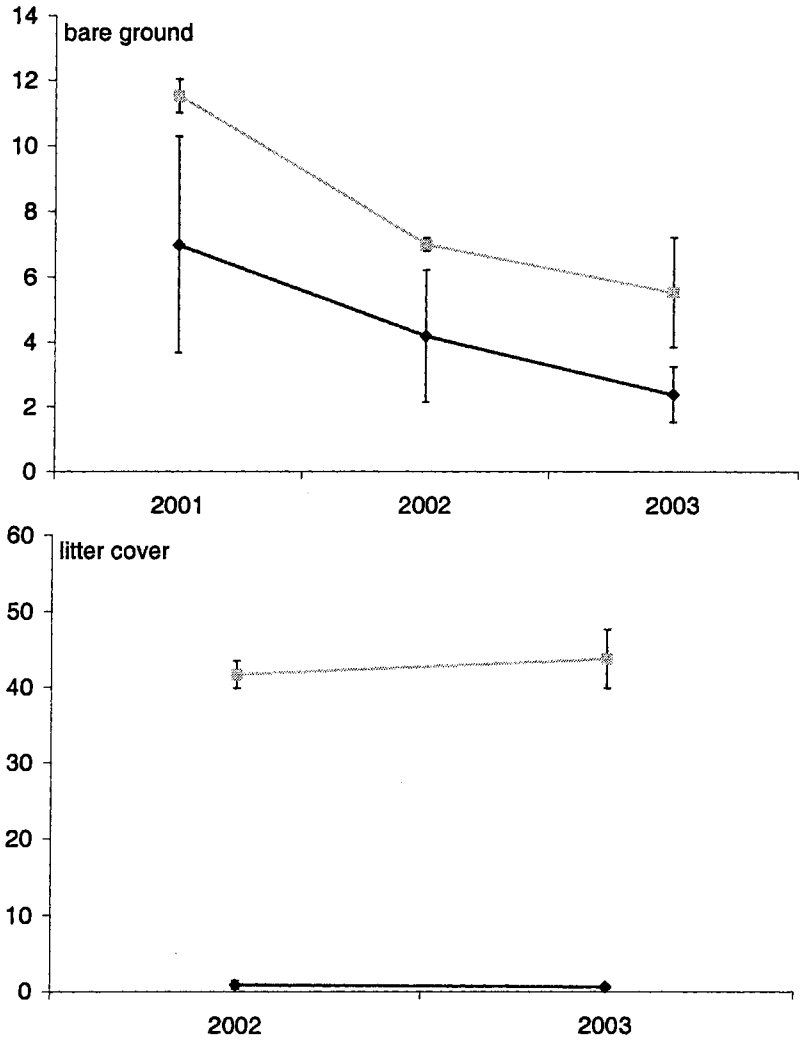

total plant cover
20
18
16
14
12
10
8
6
4
2
0
Traditional
Patch
2001
2002
2003
Schizachyrium scoparium cover
30
25
20
15
10
5
0
2001
2002
2003
forb cover
12
10
8
6
4
2
0
2001
2002
2003
Year

Figure 3 continued.



VITAE #2

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